

AN ECOLOGICAL STUDY OF EPIBIONTS ASSOCIATED WITH THE
SHELL OF THE SEA SCALLOP, PLACOPECTEN MAGELLANICUS
(GMELIN, 1791) (MOLLUSCA:PELECYPODA)

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AN ECOLOGICAL STUDY OF EPIBIONTS ASSOCIATED WITH THE SHELL
OF THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*
(GMELIN, 1791) (MOLLUSCA: PELECYPODA)

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by
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ABSTRACT

The object of the study was to describe the assemblage of epibiotic organisms associated with the shell of the sea scallop, *Placopecten magellanicus* (Gmelin, 1791). Qualitative information from approximately 3 dozen shells was combined with quantitative data obtained from 12 additional shells. The numerical data were subjected to statistical analyses in order to examine dominance, diversity and affinity within the association.

Live scallops were collected by divers from an area in St. Mary's Bay, on the southeast coast of the Island of Newfoundland. The external surfaces of the shells were examined using a dissecting microscope and the area occupied by each epibiotic species was measured. X-radiography was used to investigate the effects of boring species within the shells. A total of 74 epibiotic species of animals and plants was recorded.

The affinity studies revealed that the scallop shell supports an epibiotic community consisting of separate and distinct component communities on its upper and lower valves, each having a predictable species composition. No seasonal or depth-related effects were detected regarding the community on adult scallops over 10 years of age, but the structures of the associations on young scallops (2 and 3 years old) were different in several respects from the adult shell community.

The dominant species are sessile or sedentary in habit and are

either filter- or deposit- feeders. They are not obligate members of the community, but nevertheless reproduce and in some cases complete their entire life cycle within the community. Diversity indices obtained for the community were generally low (ranging from 0.3 to 3.6 for a single valve) and were lower for upper valves than for lower valves.

Boring species play an important role in the development of the community. Their activities modify the surface of the shell, making it more habitable for certain later-arriving species. Damage to the shell is rarely extensive and the scallop does not generally appear to suffer any harm from the presence of these or any other of the epibionts.

To
Cynthia

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Mrs. P. Bennett of Technical Typing typed the final manuscript and is therefore largely responsible for the appearance of this thesis.

Taxonomic Specialists

The author is grateful for the assistance given by the following persons in the identification of certain of the associated species. The numbers correspond to those in square brackets following the particular species, listed in Table 1.

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6. Mr. B. E. Hopper, Agriculture Canada, Ottawa.

Annelida: Polychaeta:

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INTRODUCTION

The sea scallop, *Placopecten magellanicus* (Gmelin, 1791), occurs at many locations around the coast of the island of Newfoundland. In several areas, particularly on the west coast, there are extensive beds of these scallops which have long been important in the commercial fisheries of Newfoundland and of other Atlantic provinces. However, catches have declined markedly in recent years (Squires, 1962) and studies have recently been instituted with regard to the possibility of applying the techniques of aquaculture to this species.

The general biology and the reproductive cycle of *P. magellanicus* in Newfoundland have been studied in some detail (Naidu, 1969 and 1970). The present study was undertaken as a preliminary investigation of the ecology of the sea scallop in this area. A thorough knowledge of the scallop's ecology may be essential to an understanding of the reasons for the decline of the commercial fishery, and of the measures necessary for its re-establishment.

The external surfaces of the shells of sea scallops occurring in the Newfoundland area are subject to fouling by a variety of other marine forms, several of which burrow into the shell. The fouling organisms attracted the attention of John W. Evans, who photographed many of them and carried out a qualitative radiographic study of the borers within the shell (Evans, 1969). Scott (1968) made a brief qualitative survey of the epifauna of the shell, including the borers, and produced what she regarded as a partial list of the organisms

present. The subject was clearly deserving of a more thorough treatment, so the present study was begun.

The purpose of this study is to describe, both qualitatively and quantitatively, the assemblage of organisms occurring upon and within the shell of the sea scallop, within a small area in southeastern Newfoundland. The study area, which is to be described fully under Materials and Methods, was chosen for its easy accessibility and for the presence of well-known scallop beds.

The project was seen as an interesting ecological study of a semi-isolated system set in the general benthic ecosystem. The relationships between the scallop and its associated organisms could be examined and there was ample opportunity to observe variations, if any, in the characteristics of the epiflora and epifauna of shell due to the effects of different water depths and different seasons of the year. Also important were the possible adverse effects upon the shell, created by the presence of the foulers. There were, for example, the questions of damage to the shell by the borers and of possible smothering or other harm to the scallop caused by an enveloping mass of surface foulers. Finally, it was felt that the results of the study would constitute valuable baseline data for the area concerned, which at present seems relatively free from pollution. Industrial use of land adjoining the sea has increased considerably in recent years, causing concern regarding possible pollution of the province's coastal waters. Baseline data provided by such studies as this might well prove useful in the future as a means of monitoring environmental changes.

The scallop shell as a substrate for an ecological study differs considerably from some other benthic substrata. Unlike the sea bottom of mud and sand upon which it lies, the shell provides a firm footing for those plants and animals which require one. Unlike rocks and stones which occur in some benthic environments, the scallop is alive and able to free the surface of its shell from silt deposited on it by turbulent water. Unlike some other bivalve molluscs, such as oysters and mussels, the adult sea scallop is not attached to the substrate and can therefore move away from an area which is unfavourable to it (and perhaps to the associates on its shell). The shell of a living scallop differs from any lifeless substrate in that the feeding activity of the scallop creates water currents in the vicinity of the shell, especially near the posterior edge; these currents may benefit filter-feeding organisms attached to the shell by bringing food material within their reach. This subject will be mentioned again in the Discussion.

The question of the type of relationship existing between the scallop and the organisms associated with its shell is certainly of prime importance in this study. One of the major criteria in assigning an association to a definite category is the subject of metabolic dependency. In order to prove the existence of such dependency in either the host or the associate would properly require detailed physiological and biochemical analyses which, in fact, have rarely been carried out, especially in marine molluscs. In most cases little is known beyond what has been inferred from observations.

The general term for any heterospecific association is symbiosis. It was coined in 1879 by A. DeBary to mean simply "living together" and was retained in that original sense by Cheng (1967). It is a broad ecological term covering all associations (excluding predation) in which there exists physical contact or intimate proximity between the two members. Under the heading of symbiosis, Cheng listed four main categories of associations based, as indicated above, upon the existence of metabolic dependency as well as upon other factors.

The first two categories are parasitism and mutualism, both of which involve metabolic dependency. Parasitism is one-sided in that the parasite depends upon the body tissues of the host, nutritionally or otherwise, while the host receives no benefit and may, in fact, be harmed. Mutualism consists, as the name implies, of a mutual dependency between the two members. Both parasitism and mutualism are obligatory relationships since in each case the benefitting member cannot live without the other (Cheng, 1967):

The other two categories of symbiosis as considered by Cheng are commensalism and phoresis. Neither is an obligatory relationship and neither involves metabolic dependency. Commensalism describes the situation in which one member of the association, the commensal, receives physical shelter from the host and nourishment from foods which are associated with and used by the host but which are not a part of the host. Phoresis is similar to commensalism, but does not involve use by the phoront of food which is necessarily associated with the host. The host merely provides shelter, support or transport for the phoront. The particular case in which the phoronts are located

on the external surface of the host was called epiphoresis by Cheng (1967). Cheng considered that, according to his definition, those animals which are commonly referred to as being epizootic or epizoic could be thought of as having phoretic associations with their hosts.

This study does not include an investigation of the specific food preferences of either the scallop or its associates. Many of the associates, such as the filter-feeding bivalves, may share the diet of the scallop and may therefore be rightly called commensals. Others may use entirely different food material and would more properly be called epiphoronts. As definite knowledge in this regard is lacking, it has been decided to use the more general term, epibiosis, to describe the relationships existing between the scallop and its associates. The associates will be referred to as epibionts. The term, epibionts, was used by Kórringa (1951) in reference to individual members of what he called the epifauna of the shells of oysters in the Netherlands. It includes epizoites and epiphytes, and refers to forms which may be either commensals or epiphoronts. In the particular type of epibiosis encountered in this study, the epibionts are attached not directly to the body of the host animal, but instead to a lifeless shell. However, the effect is the same in that the epibiont receives either shelter or support, as the case may be, as well as occasional transportation.

A group of species occupying a certain well-defined habitat, or living in association with a particular host organism, is regarded by some workers as constituting a 'community'.

The term, 'community', has been used in slightly different ways

by different investigators. As this term is to be used in this study, some clarification of terminology is in order. Mills (1969) reviewed the history of the development of the community concept in marine zoology. Odum (1959) also examined the subject of community ecology. Both felt that "community" should be a fairly broad term, and Odum suggested that it might be used in two different senses. First, it could be used in the sense of "a community", such as to designate a group of populations of organisms inhabiting a pine log in a forest. Alternately, it could be used in the sense of "the community", that is (to use a similar example), to designate the assemblage of organisms typically found associated with all pine logs in that forest - the "pine log community". This follows the practice of naming a biotic community according to the physical habitat of the community. It is in this latter sense that the term will be used here.

By this definition, a particular community would be expected to include the same populations (allowing for variations in rarer species), occurring in similar proportions, wherever the right habitat is found in the same area at the same time. This recognizes the fact that, due to environmental factors, similar habitats in widely-spaced geographical areas may support very different communities. Also, the community may or may not be subject to seasonal variations.

Analysis of the characteristics of communities has received considerable attention from modern ecologists, having had its beginnings in the field of plant ecology. The theory and practice of community studies have been well reviewed by previous workers. Fager (1963) dealt with the identification, description and analysis of marine

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communities. Longhurst (1964) placed special emphasis on sampling techniques. Pielou (1966) presented the first thorough mathematical analysis of the various techniques of determining species diversity within communities.

By far the greatest number of marine community studies have been limited to level, soft-bottom areas. These were well summarized up to 1953 by Thorson (1957). Other important level-bottom studies since then were reviewed by McCloskey (1969). McCloskey's own work involved the first quantitative study of the fauna associated with a coral (*Oculina arbuscula*, in North Carolina). His analysis of the diversity of the community was particularly thorough but, unfortunately, all colonial animals had to be omitted from the study because his analytical methods were based upon counting numbers of individuals.

Bénard (1960) described the epifauna of the coralline alga, *Lithophyllum*, in the region of Roscoff, France. His list of species was extensive and several zones within the alga were described.

The epifaunas of certain bivalve molluscs, especially oysters, have been studied extensively. Miyazaki (1936) described qualitatively and quantitatively the organisms fouling the oysters in an oyster farm in Kanagawa Prefecture, Japan. Lamy and André (1937) reviewed the literature dealing with boring annelids in the shells of molluscs. An extensive study of the shell of the European oyster, *Ostrea edulis* as a habitat was performed in the Netherlands by Korringa (1951).

Considerable qualitative and quantitative data were presented. Korringa mentions a classic study of animal communities occurring on German oyster beds (Möbius, 1893 - not seen). According to Korringa,

Möbius' paper dealt more with organisms found between the oysters - living freely in water or sediments, or attached to stones and other supports - than with forms using the shell of the living oyster as a habitat. Wells (1961) discussed the fauna of oyster (*Crassostrea virginica*) beds off North Carolina with particular reference to the salinity factor.

Epifaunal studies involving species of scallops other than *P. magellanicus* have been of a brief, qualitative nature. Allen (1953) described the epifauna (14 species) on upper valves of *Chlamys septemradiata* in the Clyde Sea, Scotland. The biology of *C. septemradiata* was discussed and information was given regarding preferred locations of some of the associates. Turner and Hanks (1959) discussed the presence of the polychaete annelid, *Polydora* sp., in shells of *Pecten irradians*. Wells, Wells and Gray (1964) qualitatively analysed the community on the calico scallop, *Aequipecten gibbus*, in North Carolina. They listed 112 species.

Previous studies on organisms associated with the shell of *Placopecten magellanicus* have also been brief, qualitative and descriptive only. No attempt has been made to quantify the species present or to analyze the characteristics of the association. Merrill (1961) listed several common commensal species (only the upper valves of the scallop were examined), indicating that some browse while others take shelter in crevices. Adults were reported to be more heavily fouled than younger specimens. Caddy and Chandler (1968) listed organisms associated with sea scallops dredged in the Bay of Fundy, Nova Scotia. Caddy (personal communication) has stated that his analyzed

data, when published, will deal only in a general way with all organisms found associated with the scallops in the dredge. Evans (1969) described qualitatively the borers in the shell of sea scallops taken from St. Mary's Bay, Newfoundland. Scott (1968) examined qualitatively the epifauna associated with shells of sea scallops, also from St. Mary's Bay. She listed some 45 forms, 34 of which were identified to the level of either genus or species. Several of these identifications appear doubtful in the light of the present study. Relative abundance of some of the more important species was discussed briefly, as were certain aspects of the natural history of the association.

The present study represents the first quantitative investigation of the associates of the shell of the sea scallop and the first thorough description of certain aspects of the ecology of that association.

The sea scallop, its general biological characteristics, its range and its synonymy have been fully described by Merrill (1959). However, it seems appropriate to give a brief description of the scallop shell as the substrate for this study.

The shell height (diameter measured from the dorsally-located hinge-line to the ventral edge) in the adult ranges from 12.5 cm to 20.0 cm (Merrill, 1959). Both valves have a convex curvature, the degree of curvature being greater in the upper (left) valve. The adult usually inhabits a shallow depression in the sea bottom (Evans, 1969), having only the central portion of the lower (right) valve in contact with the substrate. The sub-circular configuration of each valve is interrupted near the umbone by the presence of comparatively flat anterior and posterior projections, commonly known as auricles or 'wings' (v. Fig. 1).

FIGURE 1

THE UPPER VALVE (UV) AND LOWER VALVE (LV) OF THE SHELL OF
A SEA SCALLOP (*PLACOPECTEN MAGELLANICUS*), SHOWING
PHYSICAL FEATURES

- a: anterior edge of valve
- b: byssal notch
- d: dorsal edge of valve (hinge line)
- us: umbonal sulcus
- w: wing

u

UV

w

d

us

b

LV



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100-1000
100-1000

Separating each wing from the main body of the valve is a well-defined sulcus extending obliquely from the dorsal tip of the umbone to the lateral edge of the valve, though this sulcus is sometimes obscured, especially in older scallops, by overgrowth of a coralline alga. The dorsal margins of the two wings together mark the location of the hinge-line of the valve.

The external surface of each valve, especially in young specimens, bears numerous fine ridges radiating outward from the umbone in all directions to the free edge. Also present are equally numerous but less prominent circular markings concentric about the umbone. These circular markings have been related (Merrill, Posgay and Nichy, 1966) to annual variations in the rate of growth of the shell. The surface markings become obliterated to a greater or lesser extent as the scallop grows older, due to abrasion and to the effects of boring, nestling and surface-fouling organisms.

Taxonomic References

The following publications were found useful as reference material in the identification of certain of the epibionts associated with the scallop shells.

Protozoa:

1. Hadzi, J. 1951. Studien über folliculiniden. Dela Slovenska Akademija Znanosti in Umétnosti Hist. nat. Med. 4: 1-390. Recommended by Donald C. Matthews, University of Hawaii (since retired), as the definitive work for identification of folliculinids. Sections were translated and found helpful in confirming generic identity of *Folliculina* sp.

2. Hyman, Libbie H. 1940. The invertebrates: Protozoa through Ctenophora. Vol. I. McGraw-Hill, New York. 726 pp. Useful in the preliminary stages of identifying protozoans.

Porifera:

1. Lévi, C. 1956. Étude des *Halisarca* de Roscoff: embryologie et systématique des démosponges. Archives de Zoologie Expérimentale et Générale 93 (1): 1-181. Aided in identification of the sponge, *Halisarca* sp. (subclass Keratosa).

2. Old, M. C. 1941. The taxonomy and distribution of the boring sponges (Clionidae) along the Atlantic coast of North America. Maryland, Dept. of Research and Education, Chesapeake Biological Station, Solomons Island, Maryland, Publ. 44. 30 pp. Used for tentative identification of the boring sponge, *Cliona vastifica*.

Cnidaria:

1. Fraser, C. McL. 1921. Hydroids of the Atlantic coast of North America. University of Toronto Press, Toronto. 451 pp. Found very helpful for tentative identifications of five species of hydroids, three of which were subsequently confirmed by a specialist.

2. Russell, F. S. 1953. The medusae of the British Isles. Cambridge University Press, London. 530 pp. Also includes illustrations of some hydroid forms. Helpful in identifying the hydroid, *Stauridiosarsia producta* (Wright, 1858)

Entoprocta and Ectoprocta:

1. Organization for Economic Co-operation and Development, 1965. Catalogue of marine fouling organisms. Vol. 2. Polyzoa. Paris. 82 pp. Useful in preliminary identification of several ectoprocts.

2. Osburn, R.C. 1912. The Bryozoa of the Woods Hole region. Bull. U.S. Bur. Fish. (1910) 30: 205-266. Helpful in identification of *Barentsia* sp.
 3. Powell, N. A. 1968a. Bryozoa (Polyzoa) of Arctic Canada. J. Fish. Res. Bd. Canada 25 (11): 2269-2320. Aided in identification of *Porella aperta* and *Stomachetosella sinuosa*.
 4. Powell, N. A. 1968 b. Studies on Bryozoa (Polyzoa) of the Bay of Fundy region. II. Bryozoa from 50 fathoms. Cahiers de Biologie Marine 9: 247-259. Useful for *Lichenopora* sp. and *Amphiblestrum osburni*.
 5. Powell, N. A. and G. D. Crowell. 1967. Studies on the Bryozoa (Polyzoa) of the Bay of Fundy region. I. Bryozoa from the Intertidal zone of Minas Basin and the Bay of Fundy. Cahiers de Biologie Marine 8: 331-347. Useful for *Tegella armifera*.
 6. Smith, R. I. (ed.). 1964. Keys to marine invertebrates of the Woods Hole region. Marine Biological Laboratory, Woods Hole, Massachusetts. 208 pp. Helpful for *Stomachetosella sinuosa* and *Cylindroporella tubulosa*.
- Annelida:
1. Berkeley, Edith, and C. Berkeley. 1952. Canadian Pacific fauna. 9. Annelida. 9b (2). Polychaeta Sedentaria. University of Toronto Press. 139 pp. Useful for *Dodecaceria concharum*.
 2. Blake, J.A. 1969. Systematics and ecology of shell-boring polychaetes from New Zealand. Am. Zoologist, 9: 813-820. Helpful with Genus *Polydora*.
 3. Blake, J. A. 1971. Revision of the Genus *Polydora* from the east

coast of North America (Polychaeta: Spionidae). Smithsonian Contributions to Zoology, No. 75. 32 pp.

4. Organisation for Economic Co-operation and Development. 1967. Catalogue of main marine fouling organisms. Vol. 3. Serpulids. Paris. 79 pp. Useful for identification of members of the Genus *Spirorbis*.

5. Pettibone, Marian H. 1963. Marine polychaete worms of the New England region: 1. Families Aphroditidae through Trochochaetidae. Bull. U. S. Nat. Museum 227 (1). 356 pp. Helpful in preliminary identifications of *Eulalia viridis* and *E. bilineata*.

6. Smith, R. I. (ed.). 1964. Keys to marine invertebrates of the Woods Hole region. Marine Biological Laboratory, Woods Hole, Massachusetts. 208 pp. Useful for *Fabricia sabella* and members of the genus *Spirorbis*.

MATERIALS AND METHODS

Field Work

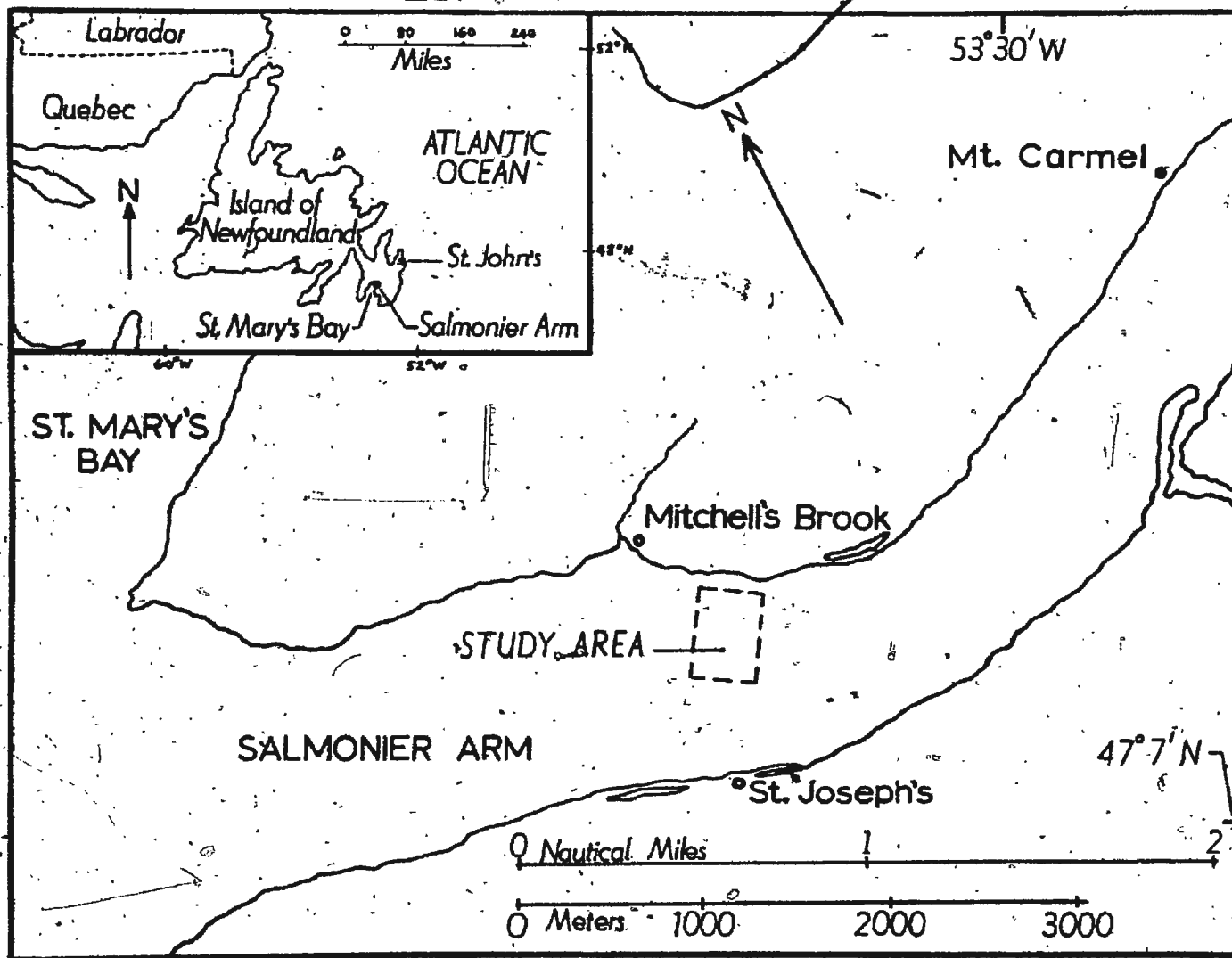
The study area is located in Salmonier Arm of St. Mary's Bay, on the Avalon Peninsula of Newfoundland, latitude $47^{\circ}7'30''\text{N}$, longitude $53^{\circ}32'\text{W}$, off the northern shore of the Arm (Fig. 2). The sea bottom there slopes downward gradually from a rocky beach to a maximum depth of about 25 meters. The bottom substrate changes rather abruptly from beach stone and gravel to a mixture of mud and sand, in which rocks occur only very infrequently. Divers report that the mud particles are loosely aggregated and therefore easily stirred up by the currents created in swimming close to the bottom. This disturbed mud, being very light, remains suspended for some time before settling back down to the bottom and is sometimes a hindrance to the divers in their work.

Besides the scallops, other typical bottom inhabitants seen by the divers were flounder, sand dollars and sea urchins. The sea urchin will be discussed later as an epibiont of the scallop.

Data from F. A. Aldrich (personal communication), Pitt (1966), and John W. Evans (personal communication) containing temperature and salinity values recorded at or adjacent to the study area indicate that the highest temperatures occur in August, average values at that time being: 15.5°C at the surface; 17.0°C at 6 m depth; and 7.2°C at 25 m depth. Average salinity at that time was 31.48‰ at 25 m. The lowest temperatures recorded are from April: 1.7°C at the surface; 0.7°C at 25 m. But it is possible that even lower values occur during the

FIGURE 2

MAP OF PART OF SALMONIER ARM, ST. MARY'S BAY, NEWFOUNDLAND, WITH
STUDY AREA INDICATED. INSET MAP SHOWS ISLAND OF NEWFOUNDLAND,
WITH APPROPRIATE LOCATIONS INDICATED



interval between December and April (for which no data are available).

Other salinity data are scanty, covering only the period from May to August. Values are generally low, ranging from 30.52‰ to 32.06‰. This is undoubtedly due to the fact that the Salmonier River and several other streams flow into the Arm.

Six collections of live scallops were made, between August 1970 and October 1971, by divers working from the shore with self-contained underwater breathing apparatus (S.C.U.B.A.). Each collection consisted of about one dozen scallops, and was taken from a depth of either 6 meters or 20 meters. The divers were in each case instructed not to choose scallops for any reason other than mere chance occurrence in their areas of search. They were not, for example, to make any efforts to obtain specimens which appeared to be particularly large, or very heavily fouled. Whether or not those instructions were carried out thoroughly is impossible to say with absolute certainty. However, it is believed that the scallops used in this study were selected without bias from the general population of the scallop beds which occur within the study area.

Two types of collection were made: mass collections and individual collections. Scallops collected en masse were transferred to trays of running seawater in the laboratory and were used for qualitative analyses of their associated populations. Scallops collected individually were placed separately into polyethylene bags at the point of collection on the sea bottom, and the bags sealed immediately with a wire closing device. These scallops were subjected to quantitative analyses.

Determination of the Age of the Scallop

A reliable method was required by which to estimate the age of each scallop examined, in order to relate the structure of the assemblage of associated species to the age of the shell. Merrill, Posgay and Nichy (1966) demonstrated that the age of a sea scallop can be accurately estimated by examining annual marks occurring on the resilium, the inner layer of the ligament uniting the two valves of the shell. These marks are duplicated on the calcareous plates which cement the rubber-like resilium into its socket, the resiliifer, and can be seen by carefully picking away the resilium. Annual marks are present also in the form of rings on the shell, concentric about the umbone. But these latter marks are often difficult to interpret due to the presence of shock rings caused by such stresses as dredging activity by fishing boats. In some cases they may even be obliterated by abrasion or by overgrowth of encrusting organisms. Growth marks on the resilium are much more legible and Merrill *et al.* found that shock marks, if present, are much less prominent there.

The age of each scallop was determined by studying the calcareous plates beneath the resilia.

Qualitative Analysis

Qualitative analyses of the epibiotic populations associated with the scallop shell were performed upon live scallops taken in mass collections. These studies were carried out as soon as possible after the scallops were brought into the laboratory, in order to minimize possible contamination of the normal assemblage by long-term exposure

to the local flora and fauna of the sea water running through the laboratory.

The scallops were collected in both summer and winter, from a depth of either 6 meters or 20 meters. An effort was made to include young adult scallops (less than five years of age) in the qualitative studies, but the efforts of divers to locate such young specimens within the study area were unsuccessful during the early stages of the study. Three young scallops were located later, in time for inclusion in the quantitative studies.

Each scallop was placed in turn in a shallow, flat-bottomed bowl and covered with sea water. The shell was examined by means of a Wild M-5 stereoscopic dissecting microscope. The first objective was to discover and identify as many as possible of the associated animals and plants. In a few cases, the identifications were accomplished fairly easily and quickly with the aid of one or more of the taxonomic keys and descriptive papers listed in the previous section. But, generally it was necessary to collect specimens and preserve them for later study. Notes were made concerning any observations made on the feeding habits, reproductive behaviour and inter-relationships of the organisms present.

The study has been arbitrarily restricted to those organisms which could be detected, examined, measured or counted readily using a dissecting stereomicroscope (though a compound microscope was also frequently used for detailed examination of mounted specimens). The lower size limit of those included is therefore of the order of 0.1 mm. Although numerous smaller organisms such as diatoms, flagellates and

Bacteria have been left untouched, it is felt that the study includes a very large proportion of the species present. Both solitary and colonial organisms are considered and a large majority of these is represented by numerical data. These have been supplemented with observations regarding behaviour and inter-relationships of many species.

Finally, information regarding two animals inhabiting the body of the scallop, observed while examining the shells, has been appended.

Investigation of the boring symbionts within the shells of the live scallops was accomplished using two techniques: direct observation and x-radiography. Certain of the shells were broken into small pieces with a hammer, and the inhabitants carefully picked out. Some specimens were badly damaged, but enough were obtained in good condition to permit positive identification of all species encountered. Experiments with such substances as orthodichlorobenzene and menthol crystals, in an effort to induce polychaete worms to emerge from their burrows in the scallop shells were generally disappointing in their results, for many did not emerge but instead died in their burrows. Scott (1968) reported similar results.

Radiography was demonstrated by Evans (1969) to be an effective technique for examining the effects of borers in scallop shells. The radiographic apparatus used in the present study was the Picker Portable Industrial X-Ray Unit, No. 6231. Medical x-ray film such as GAF HR3000 produced good results when exposed as follows: source-to-film distance, 16 cm; kilovoltage, 35 kv; milliamperage, 3 ma; time, 54 sec. The shell was placed directly on the film pack during

exposure. Slight modifications of this arrangement were required in the case of abnormally thick or very young (thin) shells. The film was processed according to the standard instructions provided by the manufacturer of the x-ray film processing chemicals. By the use of these radiographs each species of borer was related to its own type of burrow configuration.

In all, about three dozen shells of living scallops were studied qualitatively.

Quantitative Analysis

For quantitative analysis of associated species populations, preserved scallop shells were chosen. Thorough examination of the surface of a shell takes considerable time, sometimes extending over a week for a single valve. To have used live material would have involved maintaining a number of scallops, including the one being examined, in running sea water in the laboratory. Organisms might have been gained from, or lost to, this unnatural environment, thus casting doubt upon the value of the quantitative work.

The scallops had been collected individually in polyethylene bags, thus preventing exchange of free-living symbionts with other scallops collected at the same time. By enclosing sufficient water inside the bag, the scallop and its associated organisms were kept alive while being carried to the laboratory. There each scallop was removed from its bag and shucked. The sex and the condition of the gonad were noted and the soft parts were discarded. The shells were immediately fixed in 10 per cent neutralized formalin.

Twelve preserved shells, each consisting of an upper and a lower valve, were chosen at random from within appropriate collections in order to obtain the following groups:

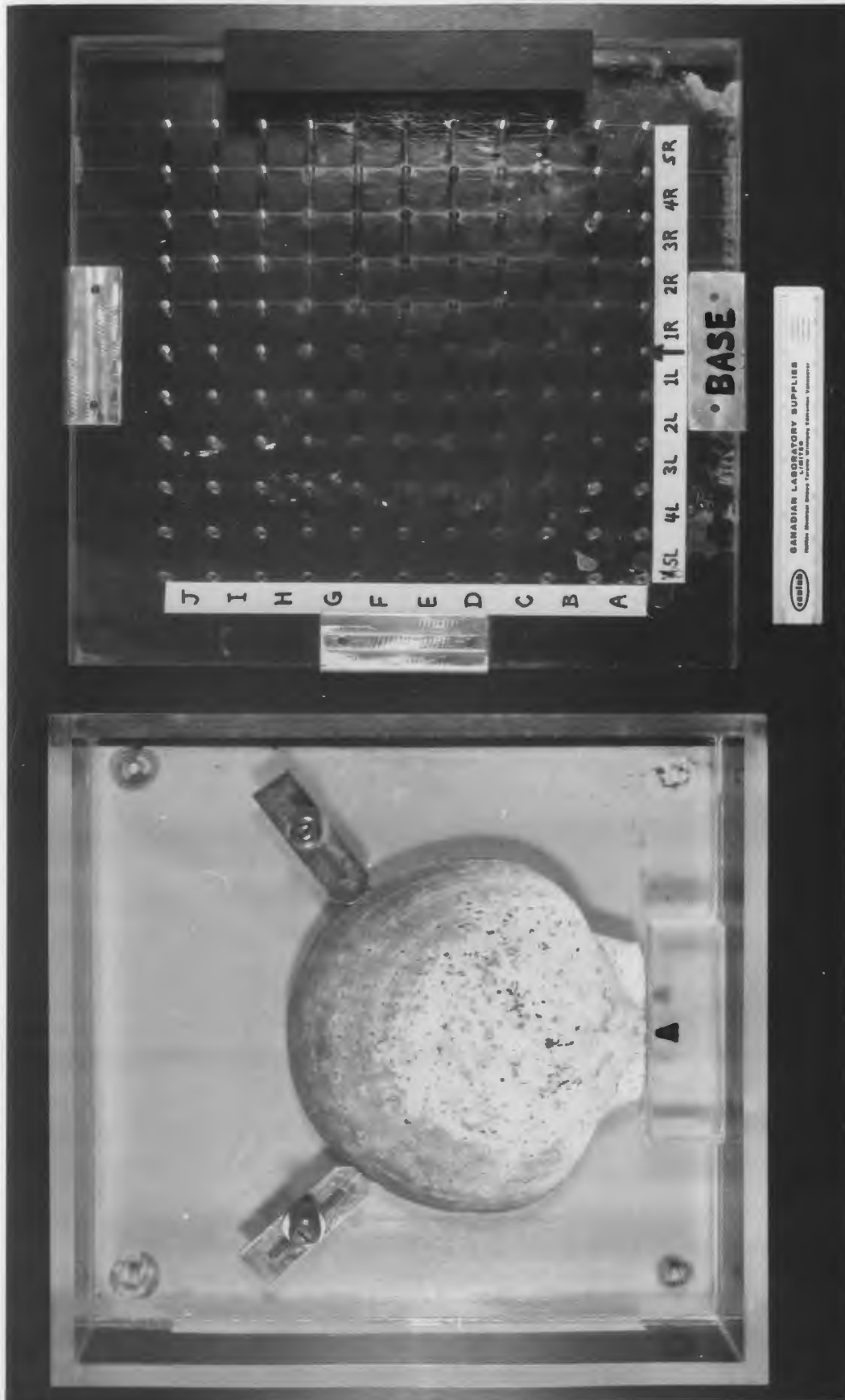
1. Five old (large) shells, all collected in summer (though not all on the same date) at a depth of 6 meters, to serve as a basis for comparison.
2. Two old shells taken in summer at 20 meters, to examine possible effects of depth upon the structure of the assemblage.
3. Two old shells collected in winter at 6 meters, to investigate seasonal differences.
4. Three young shells, taken in summer at 6 meters, in order to study early stages of the infestation of the shell.

Each of the twelve shells was given a number; these run from 1 through 12, inclusive. The dorso-ventral height and the anterior-posterior length of each valve were measured to the nearest 0.1 cm. The valve, together with its associated epibionts, was weighed to the nearest 0.1 g.

The external surface was marked with a 2 cm. grid in order to facilitate detailed examination. To accomplish this a plexiglas box was designed, the lid of which had the grid engraved on it and holes located at the intersections of the grid lines (Fig. 3). Each valve was centred against one side of the box and marked by passing an electric drill down through each hole. The marks were joined with pencil marks to complete the grid. The small portion of the surface area (about 2.5 mm^2) which was lost from each grid-square due to the presence of the drill marks was judged to be insignificant when compared

FIGURE 3

APPARATUS FOR MARKING SURFACE OF SCALLOP SHELL WITH A GRID, IN ORDER
TO FACILITATE EXAMINATION. THE LID (AT RIGHT) HAS BEEN REMOVED
TO SHOW A VALVE SECURED IN PLACE FOR MARKING WITH AN ELECTRIC
DRILL, WHICH IS GUIDED BY THE HOLES IN THE LID.



to the total area of the square (400 mm^2). Each grid-square was identified by a letter and number, as shown in Fig. 4.

For the purposes of this study the external surface of the scallop shell valve has been arbitrarily divided into three regions: umbonal, central and peripheral. The locations of these regions were suggested partly by the configuration of the valve, and partly by the patterns of distribution of certain associated organisms on the surface of the shell as revealed by preliminary investigations. The regions are defined generally as follows: The umbonal region includes the area of the umbone and the two wings; the central region occupies the middle or highest part of the valve; the remainder is included in the peripheral region, which extends from the boundary of the central region to the edge of the main body of the valve.

As applied to a particular valve, each region was defined precisely by referring to those squares which together most nearly fitted the broad definition given above. In the case of a valve of average size, such as most of those studied quantitatively, the umbonal region contained eight complete grid-squares, the central region contained 12 complete squares, and the peripheral region included from 20 to 35 complete and partial squares, depending upon the size and configuration of the valve (Fig. 5).

The surface area of each region, and hence of the entire valve, was estimated using the area of a single square (400 mm^2) as a basic unit. The valve was photographed and radiographed, then transferred to a solution of 40 per cent isopropyl alcohol.

During quantitative examination, the valve was submerged in

FIGURE 4

DIAGRAM OF ONE VALVE OF A SCALLOP SHELL SUPERIMPOSED UPON THE GRID
USED TO FACILITATE EXAMINATION OF THE SHELL SURFACE. EACH
GRID-SQUARE IS DESIGNATED BY A COMBINATION OF LETTERS
AND NUMERALS (A-1L = ROW A, COLUMN 1 LEFT, ETC.)

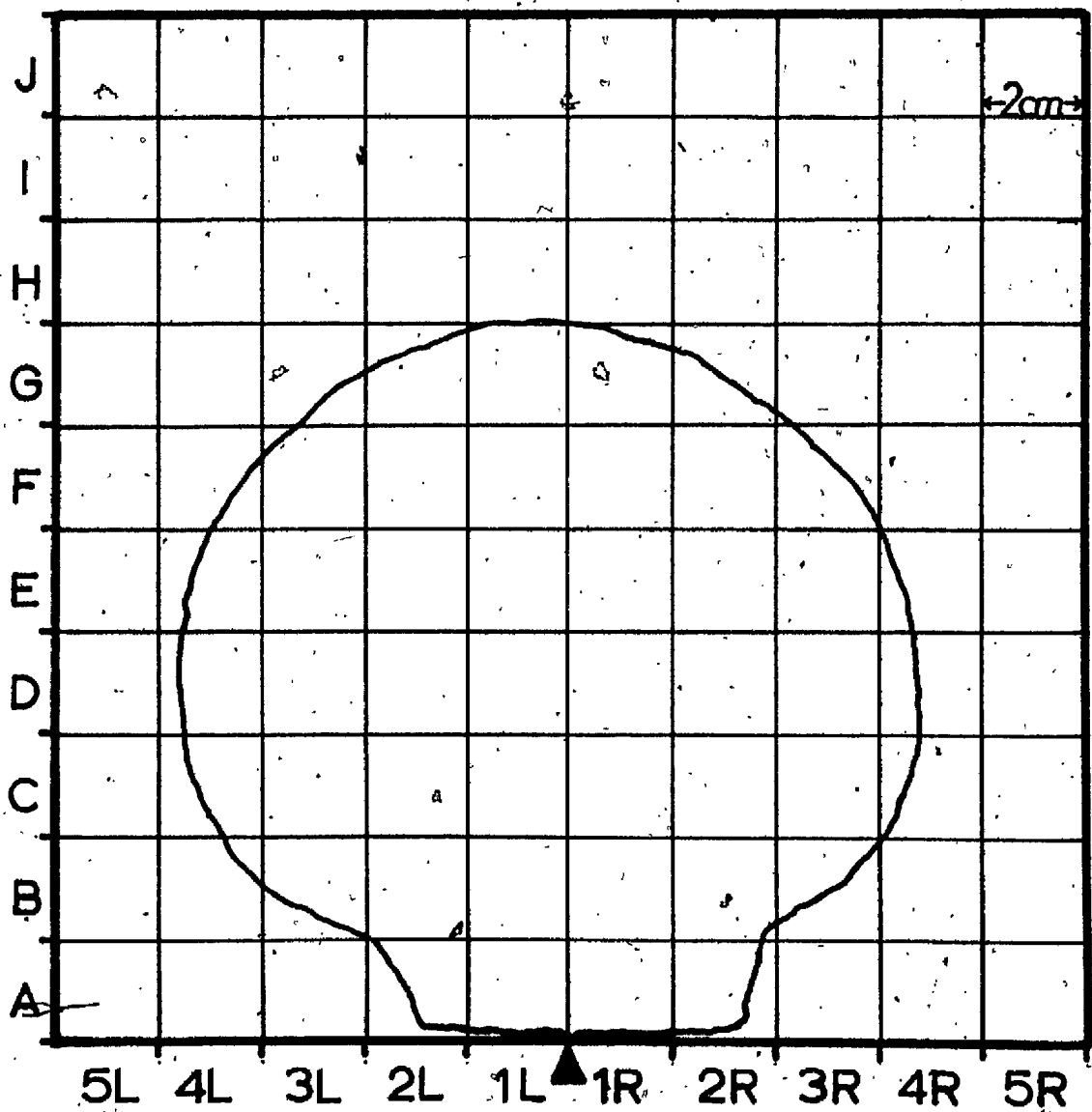


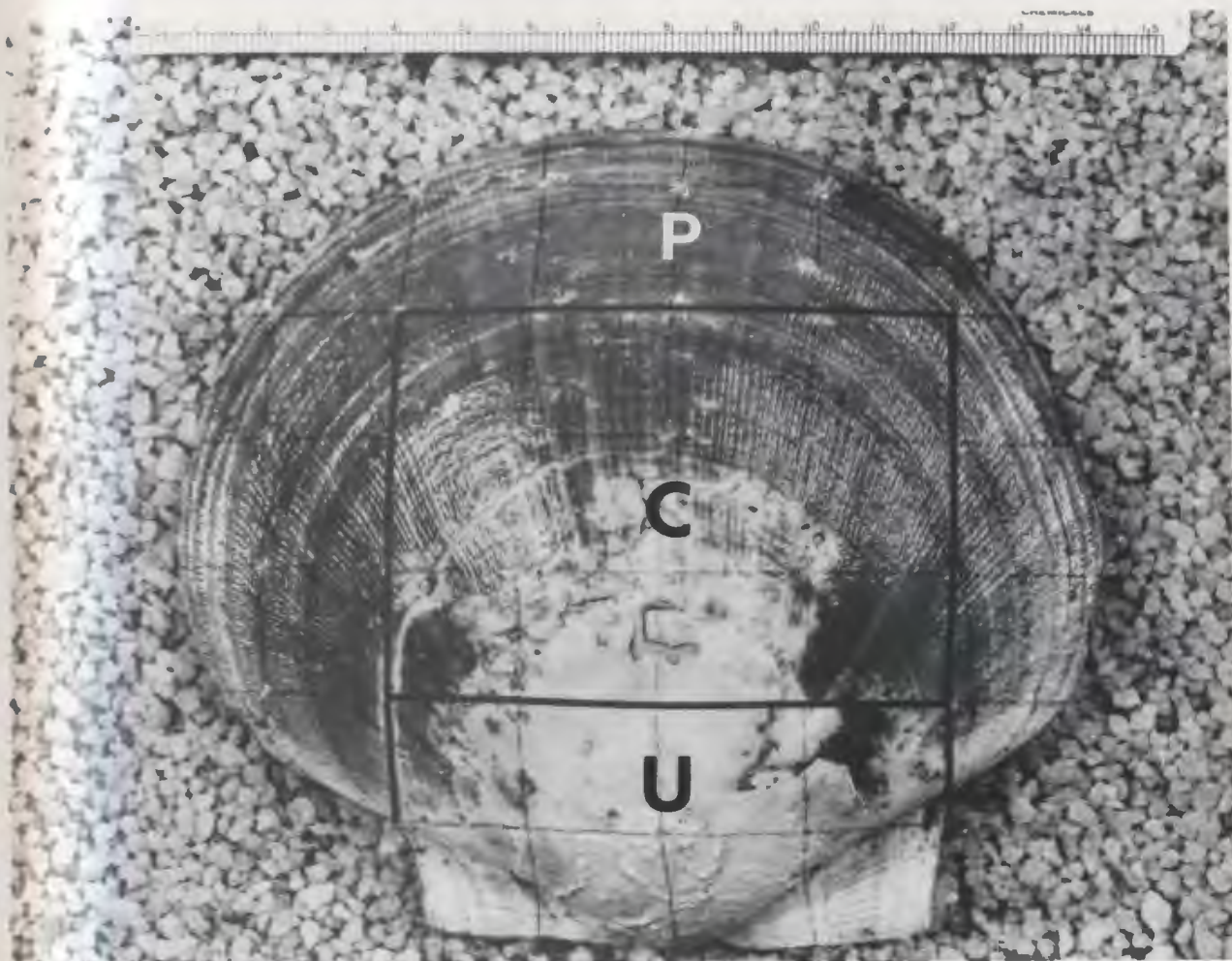
FIGURE 5

UPPER VALVE OF THE SHELL OF A SCALLOP WHICH HAS BEEN MARKED WITH THE GRID AS DESCRIBED IN FIGURE 3. LETTERS INDICATE THE THREE REGIONS INTO WHICH THE SURFACE OF EACH VALVE WAS DIVIDED IN ORDER TO STUDY THE PATTERN OF DISTRIBUTION OF THE EPIBIONTS. BLACK LINES MARK INTER-REGIONAL BOUNDARIES.

c: central region

p: peripheral region

u: umbonal region



isopropyl alcohol to avoid optical distortion and reflection. A Wild M-5 stereomicroscope was used.

The question of how to estimate the "amount" of each species on the surface of a grid-square was a serious one. To simply count the organisms would not have been satisfactory, for two reasons. First, colonial organisms such as coralline algae, sponges, ectoprocts and compound ascidians cannot be counted. They would therefore have had to be left out of the survey as was done by McCloskey (1968), thus reducing the value of the study. Second, a simple count gives no indication of the size of the organism and therefore of its effect upon the substrate. It was decided instead to measure each species' "area of influence" within the square. This was defined as follows.

Each species of epibiont present on or in the shell at any time exerts its physical influence upon the local environment of the shell and, either directly or indirectly, upon some or all of the other species present. Its total influence is the sum of the space occupied by it over its area of contact with the substrate, and of any additional space which it may encroach upon during its vital activities, especially feeding. Most of the symbionts of the scallop shell, as will be discussed later, are ciliary feeders. Their food consists of minute organisms or particles of detritus found suspended in the water or lying upon the shell surface. Many of them are undoubtedly in direct competition for the same food material and living space. During the observations on living shells it was possible, by means of a calibrated scale in one ocular of the stereomicroscope, to measure the areas covered by many of the organisms in their food-gathering activities.

A list was compiled of the regularly-occurring epibionts and their areas of influence, as follows: (i) for solitary forms, or widely-spaced individuals in a colony, whose area of attachment was greater than its feeding area (as in sponges or tunicates), the area of attachment was taken to be its area of influence; (ii) in a case where the feeding area was greater, as with a boring polychaete worm sweeping the substrate with its tentacular palps, the feeding area was used as the area of influence; (iii) for a colonial form in which the individuals were intimately joined, the area of influence was considered to be the total area of the colony. In certain solitary species the area of influence of an individual was always about the same size, so it was necessary in such a case only to count the individuals and multiply the sum by the appropriate value, rather than measure each individual.

In effect, each species was "counted" in terms of the number of units of area occupied, rather than the number of individuals present. The justification for using such a method lies in Pielou's (1966) review of modern methods of calculating diversity by the use of information content. For collections containing uncountable species, the amount of each species must instead be measured in terms of units of some quantity such as weight, volume, or area of ground covered, and the units are then treated as individuals. The "area covered" method was chosen, and was used for other purposes as well as for the calculation of diversity.

The organisms on the scallop shell, by virtue of their different heights, occupy space at various levels above the surface of the shell.

For this reason the areas occupied by different species occasionally overlap and it is thus possible that the total area occupied by all species on a densely-populated grid-square may exceed the surface area of that square, resulting in a per cent coverage figure greater than 100 per cent. This occurred only infrequently during this study and presented no problem in the analysis of the data.

In the process of counting and measuring all organisms found, the surface of each grid-square was covered many times. Each symbiont attached to, or resting upon, the surface of the shell or nestling in a crevice was noted, and the total area of occupation for each species was calculated for each square.

Boring species presented a different problem. It was necessary to assess their effect upon the surface of the shell (their "areas of influence") as well as the extent of their boring activities within the shell. There were four borers present: three species of polychaetous annelid and a boring sponge, *Cliona vastifica*. The effect of *C. vastifica* upon the surface was a large number of holes, excavated outward from its meandering galleries within the shell. These served to give its ostia and oscula access to the environment. The surface area occupied by holes was thus rendered unavailable for attachment or for food-gathering by other species, therefore the sponge's area of occupation on the surface was calculated as the product of the number of holes and the average size of a single hole.

All three polychaetes were treated alike, by observing (in the live material) the food-gathering activities of their tentacular palps in the area around the burrow opening. For each species an average

area of coverage for the palps during feeding was calculated, and this figure was used in the calculation of that worm's area of occupation on the surface. These calculations were not performed immediately because it was impossible to determine by surface examination alone the identity and number of each boring species present. Only by studying the radiograph of the corresponding section of shell could this information be obtained.

Matching a grid-square on the valve with the corresponding part of the radiograph was a simple matter, since the marks drilled in the surface of the valve appeared in the radiograph. By joining the images of the drill marks, the grid pattern was reproduced on the radiograph (Fig. 6).

Evans (1969) demonstrated that borers in the shell of the sea scallop can be identified in radiographs by virtue of the characteristic configuration of their burrows. For each grid-square, the species of polychaetes having burrows originating in the square were noted. The individuals of each species were counted and these figures were used to calculate the total area occupied at the surface of the square by each species.

It is necessary at this point to recognize the fact that a small number of the burrows observed in each radiograph may have been empty, their occupants having died. A radiograph cannot demonstrate whether or not a burrow is occupied, since the worms are soft-bodied and completely transparent to x-rays. This fact may have introduced a minor error into the calculation of the areas occupied by the worms on the shell surface. Such an error, if present at all, was unavoidable.

FIGURE 6

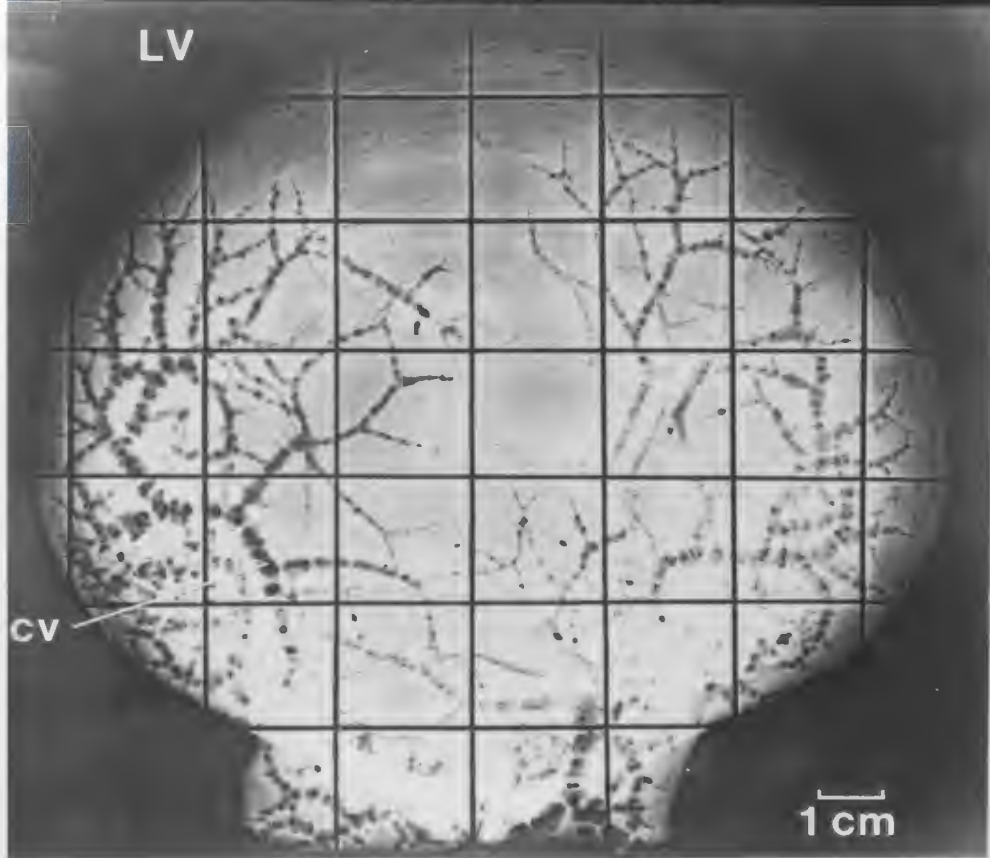
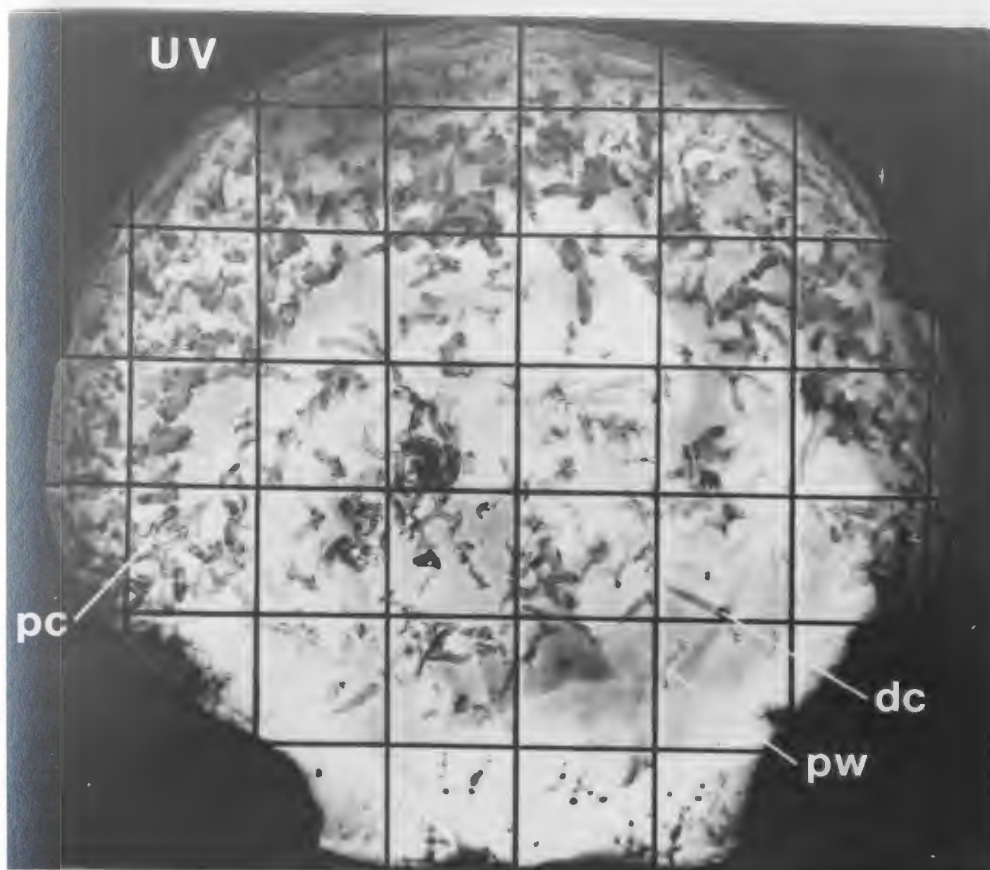
X-RADIOGRAPH OF UPPER VALVE (UV) AND LOWER VALVE (LV) OF THE SHELL OF A SCALLOP, SHOWING BURROWS CREATED BY EACH OF THE FOUR BORING EPIBIONTS RECORDED IN THIS STUDY. THE GRID CORRESPONDS TO THAT USED FOR THE EXAMINATION OF THE EXTERNAL SURFACES OF THE SAME SHELL, AND WAS USED IN ESTIMATING THE PERCENTAGE OF EXCAVATION BY THE BORERS

cv: *Cliona vastifica*

dc: *Dodecaceria concharum*

pc: *Polydora concharum*

pw: *Polydora websteri*



No practical method could be found for determining whether or not each and every one of the hundreds of polychaete burrows present in a typical valve actually contained the original occupant at the time of examination of the shell.

The radiographs of the valves were also used to obtain a rough estimate of the extent of the boring carried out within the valve by each species. A radiograph is an image of only two dimensions and is therefore unsuitable for calculating the volume of the burrows shown by it. However, it is possible instead to measure the area of each burrow as it appears in the radiograph, and to use this area as an indication of the amount of shell excavated. In practice, the area occupied by the burrows of each species within the boundaries of each grid-square, was estimated as a percentage of the total area occupied by all species within the square.

Analysis of Data

The numerical data were analyzed to yield information concerning: species composition of the assemblage, species distribution, population density, spatial dominance, diversity, and presence of recurring species groups. All of these characteristics have been widely used in numerous studies of plant and animal assemblages, and together provide essential information regarding the relative proportions of the species populations.

Analysis of the raw data began with the calculation of the shell surface area occupied by each species within each of the three regions (umbonal, central, and peripheral) of each valve, by summing the appropriate data over the constituent grid-squares of each region.

"Area occupied" values for each species over the entire valve were

obtained by simple addition of the regional figures. Next, the occupancy of each species within each region (and on each valve) was calculated as a percentage of the total area occupied in that region (or valve) by all species present. Note that the total area occupied is not necessarily the same as the total area of the region.

Dominance

Most of the animals occurring in the assemblage require space on the surface of the shell in which to live and to carry out food-gathering activity. The foregoing method of calculating area of occupation takes into account both aspects of the requirement for space. Of those species having the greatest areas of occupation, as calculated by this method, most are filter-, suspension- or deposit-feeders. These all feed upon material introduced into the environment of the shell by virtue of its being suspended in, or deposited from, the surrounding water. It seems reasonable to consider that those species, which make the heaviest demands upon the space and the food resources of the habitat, occupy positions of importance within the association. It was thus decided to measure dominance in terms of space occupied on the surface of the shell. This is comparable to evaluating dominance in a species of solitary animals in terms of the numbers of individuals present.

However, the listing of a certain species as a dominant form, based solely upon its abundance on only one shell, would present a narrow and unreliable view of the situation. It was desirable instead to establish whether the dominant epibiotic species on particular shells maintained their same relative positions of importance from one

shell to another through an entire series of shells. McCloskey (1969) described (without source reference) a method for determining dominance in a series of associations, based not only upon sheer abundance but also on the frequency of occurrence from sample to sample. The procedure is as follows.

For each scallop shell valve, the list of associated species is arranged in descending order of abundance. Each species having first place ranking is assigned 100 points; each second place species, 99 points; and so on. The number of points awarded for first place is chosen arbitrarily and need only be large enough that all species present may be included in the awarding of points. A biological index value is then calculated for each species by adding the rank points to that species for all valves. For example, a species achieving first place rank on each of 12 valves would have a biological index value, for that series of 12, of 1200. The index is therefore a reflection of the frequency with which the organism was present in the series as well as of the frequency with which it ranked highly in any one valve. Also, equal statistical weight is given to each association, regardless of its size. The species having the highest biological index values can then be arranged in descending order to obtain a list of the dominant forms for the whole series.

Following the above method, the biological index value for each species was calculated. Data from upper and lower valves were analyzed separately.

Diversity

Another commonly studied aspect of the structure of an association of organisms is its diversity, that is, the relationship between numbers of species and numbers of individuals. Of the many indices of diversity which have been proposed, the method most commonly used in recent studies is that involving the use of information content. Pielou (1966) described variations on the method to suit different types of biological collections. The assemblage associated with a scallop shell valve fits into Pielou's first category, in which the collection is small enough for all members to be identified and counted. When some or all of the organisms in a collection are of such a form (e.g., a sponge, or a colonial species) that they cannot be numerically counted, then all are instead "counted" in terms of the number of units of area occupied.

The first diversity index used for this type of collection is the diversity per individual, H , which is a measure of the uncertainty of the specific identity of a randomly-chosen individual. It is given by Brillouin's formula (Pielou, 1966):

$$H = \frac{1}{N} \log \frac{N!}{N_1! N_2! \dots N_S!},$$

where: N is the total area occupied,

S is the number of species,

N_i is the area occupied by the i th species.

Another index which is sometimes used is the total diversity,

$$B = H \times N \text{ (Pielou, 1966).}$$

The choice of the base of the logarithms in Brillouin's formula

is left to the investigator. Base 2 is most commonly used, in which case the unit of H has been named the "binary digit", or "bit".

The diversity H as just defined may be compared with the maximum possible diversity for the collection, in order to determine the evenness with which the individuals (in this case, the units of area occupied) are divided amongst the species in the collection (Pielou, 1966). For this type of collection, the maximum possible diversity per individual (Pielou, 1966) is:

$$H_{\max} = \frac{1}{N} \log \frac{N!}{\left\{ \left[\frac{N}{s} \right] ! \right\}^{s-r} \left\{ \left[\frac{N}{s} + 1 \right] ! \right\}^r},$$

where: $\left[\frac{N}{s} \right]$ is the integer part of $\frac{N}{s}$,

$$r = N - s \left[\frac{N}{s} \right].$$

The evenness, J, is then given by:

$$J = \frac{H}{H_{\max}}$$

This method was used to determine the following values for each of the 24 valves: (i) diversity per individual; (ii) the evenness component of diversity. In this case, an "individual" is a single unit of area as used in the measurement of each species' area of occupancy, i.e., one square millimeter.

Affinities Between Assemblages

In a study involving a discontinuous habitat within a certain area, the question might naturally arise as to whether that habitat has

associated with it a regular and predictable community of organisms.

In order to demonstrate that such was the case, it would be necessary to show sufficient similarity amongst the assemblages found on randomly-selected samples of the habitat. McCloskey (1969) described a method previously used by other investigators to measure the degree of similarity between pairs of assemblages, or samples.

The method involves calculating an index of affinity for the pair of samples. The index used here is defined as the sum of percentages of the species common to both samples. For each common species found, the smaller percentage area occupied (of the total occupied area) is added to a running total, which becomes the index of affinity for that pair of samples. All possible pairs of samples are similarly compared, each comparison yielding its own index. The more similar are the samples with respect to their species composition and proportions, the higher is the index.

The method involves a certain amount of subjectivity, for the investigator must decide upon a minimum acceptable value for the index of affinity, based upon the results of previous workers. If his indices lie above that minimum, he may make the assumption that there is a regular community associated with the habitat under study.

In this study, two types of pair-comparisons were made. The first was between pairs of entire valves. It was decided that valves, rather than whole shells, should be compared, in view of apparent differences between the associations of upper and lower valves. The following comparisons were made: (i) within the base group of five shells, all in the same "old" age group and from the same depth (6 m)

and season (summer), inter-shell comparisons were made by comparing first the upper valves, then the lower valves; (ii) the base group was compared with the group of two scallops from 20 m, in the same manner; (iii) the base group was similarly compared with the group of two scallops from the winter season; (iv) similar comparison of the base group with the group of three young scallops; (v) intra-scallop comparison of upper valve with lower valve, carried out for each of the twelve scallops.

The second type of comparison was made between pairs of regions on individual valves, in which each region was compared with each other region of the same valve. These comparisons were made not from the point of view of the community concept, but rather for the purpose of determining whether or not the division of the surface of the valve into three regions, made arbitrarily early in the study, was valid. If this division did reflect the pattern of distribution on the valve, it was necessary to determine the degree of similarity amongst the assemblages within the three regions.

The data regarding the activity of borers within the shell, as studied by radiography, are presented in the form of estimates of the percentage of shell material excavated within each valve, and within each region of the valve. The boring activity of each species is estimated as a percentage of the total quantity bored. No further analysis of these data was attempted.

RESULTS AND OBSERVATIONS

A total of 74 species, representing 13 phyla, was recorded from the shells of approximately four dozen scallops taken from a single study area. These include 69 animals in 11 phyla and 5 plants in 2 phyla. These are listed in Table 1, together with relevant taxonomic information and brief notes on their occurrence. Most of the species names are followed by a number in square brackets. This number refers to the taxonomic specialist whose assistance was engaged in the identification of that particular organism. The seventeen specialists are listed in the Acknowledgements section. Where no such number occurs, identification was made by the author from specimens identified previously by other local researchers, or by reference to one or more of the taxonomic publications listed in the Review of the Literature section.

Of these 74 epibionts, 53 occurred on scallop shells studied quantitatively and are therefore represented by numerical data. These are each indicated in Table 1 by an asterisk placed just before the name of the organism.

The remaining 21 species were recorded only during qualitative examination of the mass-collected scallops held in trays in the laboratory. These are not included in the quantitative data and their names appear without asterisks. At least two-thirds of them are not permanently attached to the substrate and have some degree of mobility. It is therefore possible that some of them may have been acquired from the sea water running through the laboratory.

Also discovered during the examination of certain of the "live"

TABLE 1

EPIBIOTIC ORGANISMS RECORDED FROM SHELLS OF *PLACOPECTEN MAGELLANICUS*,
FROM SALMONIER. ASTERISKS INDICATE SPECIES FOR WHICH NUMERICAL
• DATA ARE PRESENTED LATER. NUMBERS IN SQUARE BRACKETS REFER
TO TAXONOMIC SPECIALISTS LISTED IN
THE ACKNOWLEDGEMENTS SECTION

ANIMALS

PHYLUM Protozoa

CLASS Ciliata

ORDER Heterotrichida

**Folliculina* sp. [1]

-most common on lower valve, in all regions; also occurs
frequently on upper valve, especially in the umbonal
region.

**Zoothamnion* sp. [1]

-recorded from both valves, but more common on upper valve,
(all regions).

CLASS Rhizopoda

ORDER Foraminifera

**Trochammina squamata* Parker and Jones. [2]

-very common in all regions of both valves.

**Eggerella advena* (Cushman, 1922). [2]

-found in all regions; much more common in umbonal and
peripheral regions of upper valve.

PHYLUM Porifera

CLASS Demospongiae

ORDER Hadromerida

**Cliona vastifica* Hancock, 1849.

-recorded from all regions of lower valve, but most common
in umbonal region; also occurs frequently in umbonal region
of upper valve.

TABLE 1 (CONTINUED)

PHYLUM Porifera (continued)

CLASS Demospongiae (continued)

ORDER Haplosclerida

**Haliclona* sp. (possibly *H. loosanoffi* Hartman, 1958).

-common on lower valve, peripheral and umbonal regions;
rare on upper valve.

SUBCLASS Keratosa

**Halisarca* sp. (probably *H. dujardini* Johnston, 1842).

-recorded from lower valve only; most common in
peripheral and umbonal regions.

CLASS Calcarea

Leucosolenia sp.

-lower valve only, umbonal and peripheral regions.

PHYLUM Cnidaria

CLASS Hydrozoa

ORDER Hydroida

SUBORDER Gymnoblastera

*Unidentified hydroid A. (possibly *Melicerium octocostatum* (M. Sars, 1835)). [3].

-recorded from both valves, but much more common on lower
valve, especially the peripheral region.

**Stauridiosarsia producta* (Wright, 1858). [3, 4].

-recorded from all regions except the central region of
the lower valve; this is believed to be the first North
American record of this species.

**Sarsia tubulosa* (M. Sars, 1835) [3].

-lower valve, peripheral region only.

SUBORDER Calyptoblastera

**Clytia gracilis* (Sars, 1851). [3].

-fairly common on both valves; all regions except lower
central.

TABLE 1 (CONTINUED)

PHYLUM Cnidaria (continued)

SUBORDER Calyptoblastea (continued)

*Unidentified hydroid B. (possibly either: (i) hydroid of a pandeoid medusa; or (ii) a bougainvilliid). [3].

-rare; lower valve, peripheral region only.

CLASS Scyphozoa

*Unidentified scyphozoan, scyphistoma stage (probably *Aurelia* sp.). [3].

-lower valve, umbonal and peripheral regions.

CLASS Anthozoa

ORDER Zoantharia

Metridium senile (Linnaeus).

-upper valve, peripheral and umbonal regions.

PHYLUM Aschelminthes

CLASS Nematoda

**Anticoma pellucida* Bastian 1865. [5; 6].

-upper valve, peripheral regions; lower valve, umbonal and peripheral region..

PHYLUM Entoprocta

FAMILY Pedicellinidae

**Barentsia* sp. (probably *B. major* Hincks, 1888).

-lower valve only, peripheral and umbonal regions.

PHYLUM Annelida

CLASS Polychaeta

FAMILY Spionidae

**Polydora websteri* Hartman, 1943.

-very common in upper valve, all regions; occasionally in lower valve, peripheral and umbonal regions.

**Polydora concharum* Verrill, 1880.

-fairly common in upper valve, all regions; rarely in lower valve, peripheral region.

TABLE 1 (CONTINUED)

PHYLUM Annelida (continued)

FAMILY Cirratulidae

**Dodecaceria concharum* Oersted.

-upper valve only, all regions.

Cirratulus cirratus (O. F. Müller, 1776). [7].

-tube-dweller; recorded from lower valve, inhabiting old abandoned boring sponge burrow; rare.

FAMILY Serpulidae

**Spirorbis granulatus* (Linnaeus, 1767).

-fairly common on lower valve, all regions; rarely on upper valve, peripheral region.

**Spirorbis borealis* Daudin, 1800.

-mainly lower valve, especially peripheral region; very rarely on upper valve.

**Spirorbis violaceus* Levinsen, 1883.

-lower valve only, umbonal and peripheral regions.

**Spirorbis spirillum* (Linnaeus, 1758).

-fairly common on lower valve, peripheral and umbonal regions; rarely on upper valve, peripheral region.

**Spirorbis vitreus* (Fabricius, 1780).

-rare; recorded from lower valve, peripheral region only.

FAMILY Phyllodocidae

Eulalia viridis (Linnaeus, 1767).

-both valves; frequently found in old empty burrows formed by boring sponge.

Eulalia bilineata (Johnston, 1840).

-same as for *E. viridis*.

Phyllodoce maculata (Linnaeus, 1767).

-same as for *E. viridis*, but of much rarer occurrence.

TABLE 1 (CONTINUED)

PHYLUM Annelida (continued)

FAMILY Sabellidae

Fabricia sabella (Ehrenberg, 1837). [8].

-tube-dweller; both valves, inhabits old empty burrows of boring sponge; rare.

FAMILY Polynoidae

Harmothoe extenuata (Grube, 1840).

-lower valve only, crawling over shell surface; rare.

FAMILY Maldanidae

Clymenella zonalis (Verrill, 1874). (tentative identification [7]).

-tube-dweller, rare; sometimes attached to surface of shell, especially along the umbonal sulcus of the lower valve; occurs also inside old abandoned burrows, such as those produced by the boring sponge, *Cliona*.

FAMILY Terebellidae

Terebella lapidaria (Linnaeus, 1767).

-similar in occurrence to *C. zonalis*, above.

PHYLUM Mollusca

CLASS Amphineura

**Ischnochiton ruber* (Linnaeus). [9].

-recorded from both valves, but more commonly on the upper; usually in the umbonal region, on the "wings".

CLASS Gastropoda

Unidentified juvenile snail.

-upper valve; in crevices and unoccupied burrow entrances; on two shells only, in small numbers.

SUBCLASS Prosobranchia

**Acmaea testudinalis* (Miller, 1776). [9].

-rare; recorded from upper valve, umbonal region only.

TABLE 1 (CONTINUED)

PHYLUM Mollusca (continued)

SUBCLASS Prosobranchia (continued)

Puncturella noachina (Linnaeus, 1771).

-occurs infrequently in umbonal and peripheral regions of upper valve only.

CLASS Gastropoda (continued)

ORDER Nudibranchia

Onchidoris aspera (Alder and Hancock, 1842). (tentative identification of juvenile specimen [10].

-one specimen only; lower valve, peripheral region.

Trinchesia aurantia (Alder and Hancock). (tentative identification of juvenile specimen [9, 10].

-one specimen only; lower valve, umbonal region.

CLASS Pelecypoda

**Anomia simplex* Orbigny, 1845.

-occurred in all six regions, but very rarely in lower central.

**Anomia aculeata* Gmelin, 1792.

-rare; lower valve, peripheral region only.

**Hiatella arctica* (Linnaeus).

-usually found nestling in crevices or abandoned burrows of other organisms; common in all regions except lower central.

*Unidentified juvenile bivalve (too young for identification).

-fairly common; peripheral and central regions of both valves.

PHYLUM Arthropoda

CLASS Crustacea

ORDER Cirripedia

**Balanus* sp. (probably *B. balanus* (L., 1758)); these were juvenile specimens, difficult to identify specifically [11].

-recorded from both valves, but more common on upper valve, especially the peripheral and umbonal regions.

TABLE 1 (CONTINUED)

PHYLUM Arthropoda (continued)

CLASS Crustacea (continued)

ORDER Harpacticoida

**Amphiascus* sp. (possibly *A. minutus*). [12].

-lower valve only; umbonal and peripheral regions.

SUBCLASS Ostracoda

*Unidentified ostracod.

-very rare; upper valve, peripheral region.

CLASS Arachnida

ORDER Acarina

**Lohmanella falcata* (Hodge). [13].

-rare; upper valve, central and peripheral regions;
lower valve, peripheral region.

Thalassarachma sp. [13].

-two specimens only; lower valve, umbonal region.

PHYLUM Ectoprocta

CLASS Gymnolaemata

ORDER Cyclostomata

**Lichenopora* sp. [14].

-rare; all regions except lower central.

ORDER Ctenostomata

**Notella* sp.

-fairly common; recorded from all regions of both valves.

ORDER Cheilostomata

**Schizoporella auriculata* (Hassall, 1842). [14].

-lower valve only, more commonly in the umbonal region.

**Cribrilina punctata* (Hassall, 1842). [14].

-lower valve only; fairly common in all three regions,
but especially in central.

TABLE 1 (CONTINUED)

PHYLUM Ectoprocta (continued)

CLASS Gymnolaemata (continued)

ORDER Cheilostomata (continued)

**Porella aperta* (Boeck, 1862). [14].

-lower valve, umbonal and peripheral regions only.

**Porella* sp. A. [14].

-lower valve, all regions; rarely in upper valve, peripheral region.

**Porella* sp. B. [14].

-rare; lower valve, peripheral region only.

**Stomachetosella sinuosa* (Busk, 1860). [14].

-lower valve only, all three regions.

**Membranipora craticula* Alder, 1857. [14].

-fairly common; both valves, all regions; mostly on lower valve, peripheral region.

**Tegella armifera* (Hincks, 1880). [14]. (Sometimes given as *Tegella unicornis* var. *armifera*.)

-lower valve only; all three regions.

**Tegella arctica* (d'Orbigny, 1851). [14].

-rare; lower valve, peripheral region only.

**Cylindroporella tubulosa* (Norman, 1868). [14].

-lower valve only; all three regions.

**Rhamphostomella ovata* (Smitt, 1867). [14].

-lower valve, umbonal and peripheral regions.

**Amphiblestrum osburni* Powell, 1968. [14].

-rare; lower valve, peripheral and central regions.

TABLE 1 (CONTINUED)

PHYLUM Echinodermata

CLASS Ophiuroidea

Ophiopholis aculeata (Linnaeus, 1767).

-occurs occasionally on upper valve (all regions).

CLASS Echinoidea

Strongylocentrotus dröbachiensis (O. F. Müller, 1776).

-recorded from both upper and lower valves, usually in the peripheral and umbonal regions; "grazes" over the shell surface, leaving characteristic marks.

PHYLUM Chordata

SUBPHYLUM Urochordata

CLASS Ascidiacea

**Aplidium glabrum* (Verrill, 1871). [15].

-lower valve, umbonal and peripheral regions.

**Molgula complanata* Alder and Hancock, 1870. [15].

-upper valve, peripheral region; lower valve, all three regions.

**Molgula citrina* Alder and Hancock, 1848. [15].

-rare; lower valve, umbonal region only.

**Ascidia callosa* Stimpson, 1852. [15].

-lower valve, all three regions.

**Didemnum albidum* (Verrill, 1871). [15].

-lower valve, all three regions.

TABLE 1 (CONTINUED)

PLANTS

PHYLUM Rhodophyta

CLASS Rhodophyceae

ORDER Cryptonemiales

FAMILY Corallinaceae

**Lithothamnium glaciale* Kjellman. [16].

-very common on upper valve, all three regions, sometimes covering almost the entire surface of the valve; also occurs rarely on the lower valve, in the umbonal and peripheral regions.

ORDER Ceramiales

FAMILY Ceramiaceae

**Antithamnion boreale* (Gobi) Kjellman. [16, 17].

-common on both valves; all regions except the lower central.

FAMILY Rhodomelaceae

Polysiphonia urceolata (Lightf. ex Dillw.) Grev. [16, 17].

-lower valve, peripheral region.

Rhodomela confervoides (Huds.) Silva. [16, 17].

-lower valve, peripheral region.

PHYLUM Cyanophyta

CLASS Cyanophyceae

ORDER Chroococcales

FAMILY Entophysalidaceae

Entophysalis sp.

-a red-coloured blue-green alga; occurs in small patches on the surface of the coralline alga *Lithothamnium glaciale* on the upper valve.

shells were a ciliated protozoan clinging to the edge of the mantle of the scallop and a tiny rhabdocoel associated mainly with the gill filaments. As neither was directly attached to or associated with the shell, they are not discussed here but are instead treated briefly in the Appendix.

Table 2 presents the data recorded concerning the 12 individually-collected scallops and their shells which were preserved and subjected to quantitative examination of their associated organisms. All of the scallops classified as "old" were in the age range of 10 to 14 years. The "young" animals were 2, 3 and 5 years old, respectively, and therefore sufficiently separated chronologically from the older group to provide a meaningful comparison. It would have been desirable to have a larger group of young scallops, including samples to bridge the gap from 5 to 10 years of age. However, as already mentioned, young *Placcopecten* were very scarce in the study area and it was not until the late stages of the collecting work that these three specimens were located.

In Tables A.1 through A.24 (Appendix 1) are listed the epibiotic species recorded from each of the 24 scallop valve surfaces examined quantitatively. Besides the area of the valve, the total area occupied and the per cent of total area occupied, all species present have been included in order of rank by abundance, the per cent area occupied by each, and (for "countable" species) the number of individuals present in each. The latter information is included for the sake of interest only and takes no part in the data analysis.

The occupying of space has been used as the basis for determining dominant species. It is therefore logical to examine the subject

TABLE 2

DATA FOR 12 SCALLOPS USED IN QUANTITATIVE ANALYSIS
OF ASSOCIATED EPIBIOTIC ORGANISMS
(UV=UPPER VALVE; LV=LOWER VALVE)

Scallop No.	Season and Date Taken	Depth Taken (m)	Sex	Age (yr)	Shell					
					Height (cm)		Length (cm)		Weight (gm)*	
					UV	LV	UV	LV	UV	LV
1	Summer, 6/ 8/70	6	Male	13	13.5	13.3	13.9	14.0	67.2	191.1
2	Summer, 6/ 8/70	6	Female	13	13.9	13.6	14.7	14.6	103.9	115.1
3	Summer, 21/ 8/70	6	Female	12	14.7	14.4	15.5	15.6	125.1	136.1
4	Summer, 21/ 8/70	6	Male	11	13.7	13.7	14.8	14.7	100.3	99.1
5	Summer, 6/ 8/70	6	Female	11	15.0	14.2	16.1	16.1	116.8	149.9
6	Summer, 15/ 7/71	20	Female	14	14.6	14.4	15.3	15.3	126.4	131.7
7	Summer, 15/ 7/71	20	Male	10	13.1	12.7	13.9	13.9	81.8	85.6
8	Summer, 31/10/71	6	Female	5	10.9	10.7	11.5	11.4	47.8	55.9
9	Summer, 31/10/71	6	Female	3	8.5	8.4	8.5	8.5	36.2	35.6
10	Summer, 31/10/71	6	Female	2	6.4	6.3	6.3	6.3	8.3	7.9
11	Winter, 22/12/70	6	Male	14	14.5	14.0	15.1	15.1	133.5	127.4
12	Winter, 22/12/70	6	Female	11	13.0	12.6	13.5	13.5	85.3	85.0

*(Shell weight includes weight of associated organisms)

of the quantity of space occupied relative to the amount of space available on the surface of the shell. The height of the upper valve of a scallop shell is usually a little greater than that of the lower valve. This, together with the greater degree of convex curvature of the upper valve, means that for any given scallop shell the area of the external surface of the upper valve is slightly greater than that of the lower valve. On the lower valve a large part of the central region is normally resting on the substrate of the sea bottom and is therefore not available for settlement. It is therefore not surprising that the percentage of the total available area which is actually occupied and used by associated organisms is usually greater on the upper valve than on the lower (v. Table A in Appendix 1). What is perhaps a little surprising is that this happens in spite of the fact that the lower valve is always occupied by a larger number of different epibiotic species.

The percentage occupancy on the upper valves ranged from 4.22% to 129% (v. Table 3). This latter figure is the only case on an upper valve of an occupancy of greater than 100% and is due to the fact that, as explained in the Methods section, the areas of influence of different epibionts may, and often do, overlap at various levels above the surface of the shell. There was one other such case, on a lower valve. The extreme values for percentage occupancy on lower valves were 5.34% and 148%. The number of species recorded ranged from 4 to 22 on the upper valves and from 8 to 37 on the lower valves. As might be expected, there were more species present on the old shells than on the young shell. It does not follow, however, that the numbers of individuals

TABLE 3.1

TOTAL AREA, AREA OCCUPIED BY EPIBIONTS, PER CENT AREA OCCUPIED, AND NUMBER OF EPIBIOTIC SPECIES PRESENT. DATA FROM UPPER VALVES, SUMMARIZED FROM APPENDIX 1, TABLE A.

Scallop No.	Total Area of Upper Valve (cm ²)	Area Occupied (cm ²)	Per Cent Area Occupied	No. of Epibiotic Species
1	140.4	118.5	84.4	10
2	158.2	84.4	53.3	7
3	172.4	156.2	90.7	12
4	152.0	67.1	44.2	12
5	178.0	119.9	67.4	12
6	168.4	217.4	129.0	19
7	134.4	125.9	94.0	18
8	98.0	45.5	46.5	7
9	56.8	3.54	6.24	6
10	30.8	1.30	4.22	4
11	164.6	135.9	82.4	22
12	135.2	42.3	31.3	14

TABLE 3.2

TOTAL AREA, AREA OCCUPIED BY EPIBIONTS, PER CENT AREA OCCUPIED, AND NUMBER OF EPIBIOTIC SPECIES PRESENT. DATA FROM LOWER VALVES, SUMMARIZED FROM APPENDIX 1, TABLE A.

Scallop No.	Total Area of Lower Valve (cm ²)	Area Occupied (cm ²)	Per Cent Area Occupied	No. of Epibiotic Species
1	135.4	200.4	148.0	21
2	148.0	26.8	18.1	27
3	167.4	31.1	18.6	30
4	141.8	21.0	14.8	24
5	174.0	9.30	5.34	18
6	164.4	19.6	12.0	30
7	133.2	55.8	42.0	37
8	91.2	47.7	52.3	10
9	50.4	5.40	10.7	14
10	29.4	8.80	29.8	8
11	158.6	31.4	19.8	25
12	127.4	23.3	18.3	32

per species were also greater on the old shells: the lower valve of shell number 2 (age: 13 years) contained only 305 specimens of the ciliate *Folliculina* sp. (for example), but that of shell number 8 (age: 5 years) held nearly 6,000 specimens!

The generally higher percentage occupancy on upper valves was due largely to the worm *Polydora websteri* and the coralline alga *Lithothamnium glaciale*, which together usually accounted for 75 to 90 per cent of the total area occupied on upper valves.

There does not appear to be any serious competition for living and feeding space on the scallop shells. Except for the two cases mentioned above, both upper and lower valves are well below 100 per cent occupancy. Even when the unavailable space in the centre of the lower valve is taken into account, there is still ample space for the growth of existing epibionts and the settlement of new species.

The results of the radiographic study of excavation by boring organisms are presented in Table 4, including data from each valve and from each of its regions. The data concern the total excavation by all species and the per cent excavation by each species. These data have not been subjected to any further analyses because, as explained earlier, they constitute a two-dimensional interpretation of a three-dimensional situation.

It is worth noting, however, that in general the most abundant borer in the upper valves is the polychaete annelid, *Polydora websteri*, while in the lower valves the sponge, *Cliona vastifica*, is most abundant.

TABLE 4 (CONTINUED)

Scallop No.	Valve	Total Excavation (%)				Boring Species	Per Cent Excavation (based on total excavation)			
		Region			Entire Valve		Region			Entire Valve
		Um- bonal	Gen- tral	Peri- ph'l.			Um- bonal	Gen- tral	Peri- ph'l.	
3	Upper	16.2	19.3	18.9	18.5	<i>Polydora websteri</i>	56.3	70.6	50.3	57.1
						<i>Polydora concharum</i>	-	3.48	19.6	11.8
						<i>Dodecaceria concharum</i>	43.6	25.9	30.1	31.0
3	Lower	18.6	3.42	7.45	8.37	<i>Cliona vastifica</i>	100	100	100	100
4	Upper	56.1	26.7	12.3	25.8	<i>Polydora websteri</i>	4.60	21.8	80.5	27.7
						<i>Polydora concharum</i>	-	9.37	-	3.06
						<i>Dodecaceria concharum</i>	-	4.68	11.1	4.08
						<i>Cliona vastifica</i>	95.4	64.1	8.42	65.2
4	Lower	37.3	14.1	8.59	16.5	<i>Cliona vastifica</i>	100	100	100	100
5	Upper	10.4	14.1	34.8	25.0	<i>Polydora websteri</i>	46.2	46.7	79.2	71.9
						<i>Polydora concharum</i>	37.5	11.9	20.2	20.2
						<i>Dodecaceria concharum</i>	8.75	41.4	0.57	7.36
						<i>Cliona vastifica</i>	7.50	-	-	0.54
5	Lower	24.4	11.3	19.3	18.0	<i>Polydora websteri</i>	10.5	-	1.97	3.71
						<i>Cliona vastifica</i>	89.5	100	98.0	96.3

TABLE 4 (CONTINUED)

Scallop No.	Valve	Total Excavation (%)				Boring Species	Per Cent Excavation (based on total excavation)			
		Region			Entire Valve		Region			Entire Valve
		Um- bonal	Cent- ral	Peri- ph'l.			Um- bonal	Cent- ral	Peri- ph'l.	
6	Upper	15.5	16.7	42.2	30.2	<i>Polydora websteri</i>	40.7	75.2	86.8	80.7
						<i>Polydora concharum</i>	8.50	14.9	7.57	8.82
						<i>Dodecaceria concharum</i>	-	9.96	5.57	5.75
						<i>Cliona vastifica</i>	50.8	-	-	4.72
6	Lower	46.0	18.5	41.7	35.7	<i>Cliona vastifica</i>	100	100	100	100
7	Upper	16.0	18.1	18.2	17.7	<i>Polydora websteri</i>	16.4	78.4	93.7	72.3
						<i>Polydora concharum</i>	12.3	12.9	4.30	9.08
						<i>Dodecaceria concharum</i>	8.23	8.71	1.96	5.72
						<i>Cliona vastifica</i>	63.0	-	-	12.9
7	Lower	22.0	2.58	0.58	6.06	<i>Polydora websteri</i>	-	-	25.0	0.99
						<i>Cliona vastifica</i>	100	100	75.0	99.0
8	Upper	17.5	0.00	1.15	2.20	<i>Polydora websteri</i>	-	-	100	35.1
						<i>Cliona vastifica</i>	100	-	-	64.8
8	Lower	45.0	20.0	0.18	9.32	<i>Polydora websteri</i>	-	-	79.1	0.94
						<i>Cliona vastifica</i>	100	100	20.6	99.0

TABLE 4 (CONTINUED)

Scallop No.	Valve	Total Excavation (%)				Boring Species	Per Cent Excavation (based on total excavation)			
		Region			Entire Valve		Region			Entire Valve
		Um- bonal	Cen- tral	Peri- ph'l.			Um- bonal	Cen- tral	Peri- ph'l.	
9	Upper	0.00	0.003	0.00	0.001	<i>Polydora websteri</i>	-	100	-	100
9	Lower	2.00	0.00	0.00	0.32	<i>Cliona vastifica</i>	100	-	-	100
10	Upper	0.00	0.00	0.00	0.00	- -				
10	Lower	0.00	0.00	0.00	0.00	- -				
11	Upper	46.2	17.8	12.6	20.5	<i>Polydora websteri</i>	2.23	23.3	76.7	31.4
						<i>Polydora concharum</i>	-	7.00	5.56	3.56
						<i>Dodecaceria concharum</i>	-	1.87	0.37	0.59
						<i>Cliona vastifica</i>	97.8	67.8	17.4	64.4
11	Lower	28.7	8.58	15.4	16.0	<i>Cliona vastifica</i>	100	100	100	100
12	Upper	11.8	17.4	2.44	9.95	<i>Polydora websteri</i>	21.3	15.8	88.9	24.7
						<i>Polydora concharum</i>	58.5	79.4	-	65.6
						<i>Dodecaceria concharum</i>	12.8	4.80	11.3	7.66
						<i>Cliona vastifica</i>	7.45	-	-	2.09
12	Lower	10.8	2.67	2.13	4.43	<i>Polydora websteri</i>	9.58	-	-	5.64
						<i>Cliona vastifica</i>	90.4	100	100	94.3

Natural History

A complete description of the assemblage of epibiotic organisms associated with the shell of the sea scallop would require a description of each species, its habits, and its inter-relationships with the other members of the assemblage. Such a lengthy, detailed account would be impractical and largely unnecessary, since many of the organisms occupy positions of relative unimportance within the association. An adequate picture can be obtained instead by examining the habits, in particular the feeding habits, of those species which dominate the living space. There are many other aspects of the life of the association which could be studied, but in a preliminary study such as this, feeding habits are most obvious and easiest to examine and, as we shall see, closely related to the reasons for the existence of the association.

In the following account, the dominant species are considered in the same order in which they occur in Table 12. That order is based upon the order in which they appear in Tables 5.2 and 5.3, which presents the dominant species recorded from upper and lower valves, respectively.

Eight of the sixteen dominant species listed in Table 12 are filter- or suspension- feeders, feeding on either zoo- or phytoplankton or detritus suspended in the water above the surface of the shell upon which they are epizootic. These include *Folliculina* sp., a suspension-feeder, and the filter-feeders *Cliona vastifica*, *Hiatella arctica*, *Membranipora craticula*, *Cribrilina punctata*, *Spirorbis granulatus*, *Spirorbis spirillum* and *Noella* sp. Two of the dominants, the foraminiferans, are primarily deposit-feeders, gathering detritus and

organic material from the shell surface. Three others, the boring polychaetes, alternate between suspension- and deposit- feeding, as the situation demands. The nematode, *Anticoma pellucida*, may be either a deposit-feeder or a carnivore, or both. The last two dominants are red algae. Most of the dominant species, then, use the same feeding method and therefore are in competition for space in which to carry on their feeding activities.

The encrusting red coralline alga, *Lithothamnium glaciale*, is found living on nearly every scallop collected in the study area. More common on the upper valve, it first appears in the region of the umbone and spreads outward in all directions, sometimes to the point of covering the entire surface of the valve. In doing so it completely surrounds the openings of the burrows of *Polydora*, *Dodeaceria* and *Cliona*. It is often found to have spread downward over the hinge area and established itself on the lower valve, where it is usually confined to the umbonal region of the shell.

The spionid polychaete worms *Polydora websteri* and *Polydora concharum* are also found almost universally in the upper valve of the scallop shells. They are similar in their habits, in that both live in a burrow of their own construction and feed by sweeping the shell surface with their tentacular palps. The two species are often located so close together that the areas covered by their palps may overlap. *P. websteri* is much more numerous than *P. concharum*, and their burrows can be differentiated radiographically (Evans, 1969). *P. websteri* occurs occasionally in the lower valve also, but *P. concharum* only very rarely.

Trochammina squamata is a foraminiferan which occurs in large numbers in all three regions of both upper and lower valves. When the entire shell (both valves) is considered as a unit, as in Table 5.1, this animal heads the list of dominants, despite its small size (approximately 0.01 mm^2 in area). It is found on relatively bare shell surfaces as well as in areas crowded with other organisms. On upper valves it favours the peripheral region, while on lower valves it appears fairly evenly distributed. Although feeding in *T. squamata* has not been observed during this study, it may be assumed that it does so by engulfment of tiny unicellular organisms and organic particles, by means of protoplasmic extensions (pseudopodia), as discussed for foraminiferans in general by Barnes (1963, p. 25).

The cirratulid polychaete, *Dodecaceria concharum*, commonly settles in old empty burrows of some other borer and enlarges and modifies them to suit its own requirements. It is found in this sort of situation within all three regions of the upper valve, but was not recorded from any lower valve. On one occasion a very small (probably juvenile) specimen was found enclosed in a sand-tube, lying on the surface of the upper valve, along the umbonal sulcus. Normally, however, the worm lies within its burrow and feeds by sweeping the shell surface around the burrow opening with its tentacular palps, in a manner similar to that of *Polydora*. However, its palps are much longer and cover about ten times as great an area as do those of *P. websteri*.

Cliona vastifica is one of a family of boring sponges known from many different calcareous substrates. *C. vastifica* is a dominant species in both upper and lower valves, but is more abundant in lower valves.

TABLE 5.1

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES
RECORDED FROM THE ENTIRE SHELLS (BOTH
VALVES CONSIDERED TOGETHER) OF THE
12 SCALLOPS LISTED IN TABLE 2.

Rank	Species	Biological Index Value (maximum: 2400)
1	<i>Trochammina squamata</i>	1970
2	<i>Folliculina</i> sp.	1927
3	<i>Cliona vastifica</i>	1910
4	<i>Polydora websteri</i>	1653
5	<i>Lithothamnium glaciale</i>	1478
6	<i>Hiatella arctica</i>	1471
7	<i>Membranipora craticula</i>	1394
8	<i>Antithamnion boreale</i>	1280
9	<i>Anticoma pellucida</i>	1192
10	<i>Eggerella advena</i>	1155

The sponge first appears in the umbonal region of the lower valve and then extends its galleries outward in branching form toward the edges of the valve. It then spreads over the hinge area and invades the upper valve. It is recognized by its perforations in the external surface of the shell, through which the sulphur-yellow colour of the sponge can be seen. These holes, averaging about 0.2 mm^2 in area, are commonly surrounded by particles of shell material removed by the sponge in the process of enlarging its burrow. The mechanism of boring by the species *Cliona* in calcareous objects is discussed by Warburton (1958a).

In several of the older scallops (over 12 years) there was evidence that *Cliona* had pierced the inner surface of the lower valve. In most instances, these holes had been repaired by the scallop through the deposition of new shell material; however, a few of the perforations had occurred in the area of the umbone, underneath the hinge ligament where it was not possible for the scallop to lay down new shell, and these holes had remained. Generally, the older scallops examined throughout the study suffered from more serious infestations of *Cliona*. In some cases the degree of chambering within the wings of the umbonal regions was so serious that pieces of the outer crust of the shell would break off easily at the slightest handling, exposing the irregular honeycomb of galleries underneath. This occurred most readily along the hinge line and it therefore seems possible that such a condition, if it progressed far enough, could result in a discontinuity of the hinge connection and hence to a loss of normal function of the shell. Such an animal would be more susceptible to predation and would probably not

TABLE 5.2

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES
RECORDED FROM THE UPPER VALVES OF THE
12 SCALLOPS LISTED IN TABLE 2

Rank	Species	Biological Index Value (maximum: 1200)
1	<i>Lithothamnium glaciale</i>	1191
2	<i>Polydora websteri</i>	1096
3	<i>Trochammina squamata</i>	994
4	<i>Dodecaceria concharum</i>	980
5	<i>Polydora concharum</i>	875
6	<i>Cliona vastifica</i>	854
7	<i>Eggerella advena</i>	804
8	<i>Folliculina</i> (sp.)	746
9	<i>Hiatella arctica</i>	729
10	<i>Anticoma pellucida</i>	541

survive long in its natural habitat.

The other foraminiferan encountered during the study, *Eggerella* *divena*, is also much more important than its small size might indicate, for it also accounted for a large proportion of the total occupied area of some of the shells. Though found in all regions of both valves, it was much more common in the umbonal and peripheral regions of the upper valves. This animal was usually found partially covered by debris, lying in a crevice or depression such as that surrounding the sand tubes at the entrance of a *Polydora* burrow.

The ciliate, *Folliculina* sp., with its green, vase-shaped lorica, was one of the most familiar epibionts attached to the surface of the shell, and occurred in larger numbers (v. Table 3) than did any other countable organism. Though sometimes attached to a relatively smooth surface, these tiny filter-feeders seemed to prefer the grooves commonly found along the growth-lines of the shell, or the empty zooecia of dead ectoproct colonies. They were more common on the lower valve, in all three regions, but also occurred frequently on the upper valve, especially in the umbonal region.

Hiatella arctica is widely known as a borer in shells, rock, and even concrete. On the scallop shells it appeared generally as a "nestler" in abandoned burrows, which it enlarged to accommodate its increasing size. Typically, it was attached to the sides of the hole by its byssal threads. It was common in all regions of the upper valve, and in the umbonal and peripheral regions of the lower valve. Many of the specimens found were small in size and were probably young.

Anticoma pellucida was the nematode found most frequently on

TABLE 5.3

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES
RECORDED FROM THE LOWER VALVES OF THE
12 SCALLOPS LISTED IN TABLE 2.

Rank	Species	Biological Index Value (maximum: 1200)
1	<i>Folliculina</i> sp.	1181
2	<i>Membranipora craticula</i>	1118
3	<i>Cliona vastifica</i>	1056
4	<i>Cribrilina punctata</i>	1005
5	<i>Trochammina squamata</i>	976
6	<i>Antithamnion boreale</i>	811
7	<i>Spirorbis granulatus</i>	809
8	<i>Spirorbis spirillum</i>	745
9	<i>Hiatella arctica</i>	742
10	<i>Nolella</i> sp.	723

the scallop shells. A very small number of minute specimens were found on one or two shells, but these could not be identified with certainty and have not been included in the data. They may well have been juvenile specimens of *Anticoma*. The nematodes were usually found underneath other organisms, such as sponges and ascidians, or amongst debris associated with algae or the stolons of colonial hydroids. On the upper valve they occurred only in the peripheral region, while on the lower valve they were also found near the umbone. They were noticeably less abundant in the winter samples.

Membranipora craticula was the most abundant ectoproct, and ranked second amongst the dominants of the lower valves of the 12 scallops included in the quantitative study. This epibiont occurred on all parts of both upper and lower valves, but was most common in the peripheral region of the lower valve. Like others of its phylum, this species is a suspension-feeder.

The other common ectoproct, *Cribrilina punctata*, was found only on the lower valve and there favoured the central region.

The filamentous red alga, *Antithamnion boreale*, was found frequently on both valves, but was a dominant species only on the lower valve, where it occurred everywhere except in the central region.

Five species of the serpulid, polychaete genus *Spirorbis* were encountered during the study. Of these, the only dominant forms were *S. granulatus* and *S. spirillum*. Both were much more commonly found on the lower valve, but also occurred rarely on the upper valve in the peripheral region. Both are suspension-feeders.

A third ectoproct, *Nolella* sp., was seen frequently everywhere.

TABLE 5.4

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES RECORDED FROM THE UPPER VALVES OF THE 5 SCALLOPS INCLUDED IN THE "BASE" GROUP ("OLD"/SUMMER/6 METERS), AND NUMBERED 1 THROUGH 5

Rank	Species	Biological Index Value (Maximum: 500)
1	<i>Polydora websteri</i>	500
2	<i>Lithothamnium glaciale</i>	494
3	<i>Dodecaceria concharum</i>	489
4	<i>Polydora concharum</i>	486
5	<i>Cliona vastifica</i>	382
6	<i>Hiatella arctica</i>	378
7	<i>Anticoma pellucida</i>	374
8	<i>Eggerella advena</i>	369
9	<i>Trochammina squamata</i>	367
10	<i>Folliculina</i> sp.	276

on the shell. This was the only other dominant besides *A. pellucida* which showed evidence of periodic occurrence; it was not recorded from the winter-collected shells.

Certain other species, while not sufficiently abundant to appear in the lists of dominant forms for the entire series of scallops, did qualify as dominants within the sub-groups and should therefore be mentioned. Amongst these are three species which were important on the lower valves of the five shells included in the base group (Table 5.5).

The scyphistoma stage of a scyphozoan (not identified positively, but believed to be *Aurelia* sp.) occurred only on lower valves collected in shallow water, and seemed to prefer the umbonal region of the valve. It was recorded from both summer- (August) and winter- (December) collected shells, indicating a lengthy period of existence, but in neither case did it exhibit strobilization. Two ectoprocts, *Porella aperta* and *Schizoporella auriculata*, also occurred on lower valves only, preferring the umbonal region.

Amongst the dominants from the deep-water (20 m.) shells (v. Tables 5.6 and 5.7), seven species have not yet been mentioned. The barnacle, *Balanus* sp. (probably *B. balanus*), was recorded from both valves but was more common on the upper valve. It was attached both to smooth surfaces and within hollows and crevices, mainly in the peripheral and umbonal regions. It is a filter-feeder, obtaining food by sweeping the water above it with modified thoracic appendages.

The hydroid *Stauridiosarsia producta* was found everywhere except the central region of the lower valve. This is believed by D. R. Calder

TABLE 5.5

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES RECORDED
FROM THE LOWER VALVES OF THE 5 SCALLOPS INCLUDED IN THE
"BASE" GROUP ("OLD"/SUMMER/6 METERS), AND NUMBERED
1 THROUGH 5

Rank	Species	Biological Index Value (maximum: 500)
1	<i>Folliculina</i> sp.	488
2	<i>Cliona vastifica</i> <i>Cribrilina punctata</i>	477
3	<i>Nolella</i> sp.	454
4	<i>Membranipora craticula</i>	451
5	<i>Spirorbis granulatus</i>	437
6	Unidentified scyphozoan	428
7	<i>Trochammina squamata</i>	400
8	<i>Porcella aperta</i>	381
9	<i>Schizoporella auriculata</i>	374
10	<i>Antithamnion boreale</i>	361

TABLE 5.6

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES RECORDED
FROM THE UPPER VALVES OF THE 2, SCALLOPS TAKEN AT A
LOWER DEPTH (20 METERS); NUMBERED 6 AND 7.

Rank	Species	Biological Index Value (maximum: 200)
1	<i>Lithothamnium glaciale</i> <i>Polydora websteri</i>	199
2	<i>Dodecaceria concharum</i>	197
3	<i>Polydora concharum</i>	195
4	<i>Cliona vastifica</i>	188
5	<i>Nolella</i> sp. <i>Balanus</i> sp.	187
6	<i>Antithamnion boreale</i>	184
7	<i>Hiatella arctica</i>	178
8	<i>Stauridiosarsia producta</i>	177
9	<i>Eggerella advena</i>	171
10	Unidentified bivalve	169

TABLE 5.7

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES RECORDED
FROM THE LOWER VALVES OF THE 2 SCALLOPS TAKEN AT A
LOWER DEPTH (20 METERS), NUMBERED 6 AND 7

Rank	Species	Biological Index Value (maximum: 200)
1	<i>Haliclona</i> sp.	200
2	<i>Folliculina</i> sp. <i>Cliona vastifica</i>	196
3	<i>Rhaphostomella ovata</i>	188
4	<i>Spirorbis granulatus</i>	185
5	<i>Membranipora craticula</i>	184
6	<i>Porella aperta</i>	181
7	<i>Nolella</i> sp. <i>Stomachetosella sinuosa</i>	179
8	<i>Antithamnion boreale</i>	174
9	<i>Didemnum albidum</i>	173
10	<i>Cribrilina punctata</i>	166

(personal communication) to be the first North American record of this species.

The haplosclerid sponge, *Haliclona* sp. (possibly *H. loosanoffi*), was a common occupant of lower valves but occurred only very rarely on upper valves. It forms a low-profiled tan-coloured carpet over large areas of shell surface, surrounding (and often covering) small attached organisms such as hydroids, entoprocts and folliculinids. The colonial ascidian, *Didemnum albidum*, with its distinctive white stellate spicules, occurred on lower valves only. A juvenile bivalve, too immature to identify even generically, was common in crevices on both upper and lower valves. Finally, two other ectoprocts were dominants in the deep-water group of shells. *Rhynchostomella ovata* and *Stomachetosella sinuosa* each occurred on lower valves only.

Amongst the winter-collected shells, six other species appeared as dominants (v. Tables 5.8 and 5.9). The serpulid polychaete, *Spirorbis borealis* was recorded mainly from the lower valve, especially in the peripheral region. The pelecypod, *Anomia simplex* (the "smooth jingle"), occurred in all regions of both valves, though rarely in the lower central region; in one case, two specimens had apparently been attached to the scallop for some time, for the shell surface all around the *Anomia* was worn fairly smooth, while the areas covered by the lower valves of the *Anomia* had retained the original configuration of concentric ridges and radial markings. A spicule-less sponge (Subclass Keratosa), *Halisarca* sp. (probably *H. dujardini*), occurred in small, low-profiled, tan-coloured patches on certain lower valves only, most commonly in the peripheral and umbonal regions. Three other species

TABLE 5.8

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES RECORDED
FROM THE UPPER VALVES OF THE 2 SCALLOPS TAKEN IN THE
WINTER SEASON (6 METERS DEPTH), NUMBERED 11 AND 12

Rank	Species	Biological Index Value (maximum: 200)
1	<i>Lithothamnium glaciale</i> <i>Polydora websteri</i>	199
2	<i>Dodecaceria concharum</i>	196
3	<i>Polydora concharum</i>	194
4	<i>Folliculina</i> sp.	190
5	<i>Cliona vastifica</i> <i>Spirorbis borealis</i>	187
6	<i>Anomia simplex</i> <i>Antithamnion boreale</i>	185
7	<i>Membranipora craticula</i>	180
8	<i>Hiatella arctica</i> <i>Lichenopora</i> sp. <i>Trochammina squamata</i>	173
9	<i>Eggerella advena</i>	169
10	<i>Spirorbis granulatus</i>	94

TABLE 5.9

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES RECORDED
FROM THE LOWER VALVES OF THE 2 SCALLOPS TAKEN IN THE
WINTER SEASON (6 METERS DEPTH), NUMBERED 11 AND 12

Rank	Species	Biological Index Value (maximum: 200)
1	<i>Folliculina</i> sp. <i>Haliclona</i> sp.	198
2	<i>Membranipora craticula</i>	191
3	<i>Porella</i> sp. A	190
4	<i>Cliona vastifica</i>	189
5	<i>Halisarca</i> sp. <i>Spirorbis granulatus</i>	187
6	<i>Schizoporella auriculata</i> <i>Stomachetosella sinuosa</i> <i>Tegella armifera</i>	182
7	<i>Antithamnion boreale</i>	178
8	<i>Cribrilina punctata</i> <i>Lichenopora</i> sp.	174
9	<i>Didemnum albidum</i>	173
10	<i>Anomia simplex</i>	164

of ectoprocts were dominants in the winter group: *Lichenopora* sp. occurred in all regions, except the central region of the lower valve; *Porella* sp. A was found mainly on the lower valve and only rarely on the upper; and *Tegella armifera* appeared on the lower valve only.

On the young shells (v. Tables 5.10 and 5.11), only two further species occupied positions of dominance. The calyptoblastic hydroid *Clytia gracilis* was fairly common on both valves, occurring everywhere except in the lower central region; its absence from that part of the shell (which lies on or close to the substrate of the sea bottom) is to be expected in an organism which stands well above the surface of the shell. *Barentsia* sp. (probably *B. major*) is the only entoproct recorded from the scallop shells examined during this study. This animal was absent from the "base" and "winter" groups, and occurred only rarely in the "deep water" group of shells. Amongst the "young" shells, however, it shared with the boring sponge, *C. vastifica* the fourth position of rank in the list of dominant forms from the lower valves. *Barentsia* usually occurred in groups of from two to a dozen individuals, and appeared to prefer attachment along grooves and crevices. It was recorded from the lower valve only, in the peripheral and umbonal regions.

Several other epibionts should also be mentioned, although none is represented here by numerical data. These were recorded, together with other less common species, from shells of live scallops maintained in the laboratory, but were not found on the preserved shells chosen for quantitative examination.

A calcareous sponge, *Leucosolenia* sp., occurred on some lower valves, in the umbonal and peripheral regions; a favourite location

TABLE 5.10

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES RECORDED
FROM THE UPPER VALVES OF THE 3 "YOUNG" SCALLOPS
(SUMMER/6 METERS), NUMBERED 8, 9 AND 10

Rank	Species	Biological Index Value (maximum: 300)
1	<i>Lithothamnium glaciale</i>	299
2	<i>Trochammia squamata</i>	286
3	<i>Polydora websteri</i>	198
4	<i>Folliculina</i> sp.	195
5	<i>Clytia gracilis</i>	194
6	<i>Antithamnion boreale</i>	100
7	<i>Dodecaceria concharum</i>	98
8	<i>Cliona vastifica</i>	97
9	<i>Membranipora craticula</i>	96
10	<i>Eggerella advena</i>	95

TABLE 5.11

SPATIAL DOMINANCE. TEN DOMINANT EPIBIOTIC SPECIES RECORDED
FROM THE LOWER VALVES OF THE 3 "YOUNG" SCALLOPS
(SUMMER/6 METERS), NUMBERED 8, 9 AND 10

Rank	Species	Biological Index Value (maximum: 300)
1	<i>Folliculina</i> sp.	299
2	<i>Membranipora craticula</i>	292
3	<i>Trochammina squamata</i>	271
4	<i>Barentsia</i> sp. <i>Cliona vastifica</i>	194
5	<i>Cribrilina punctata</i>	188
6	<i>Hiatella arctica</i>	186
7	<i>Clytia gracilis</i>	183
8	<i>Halisarca</i> sp.	100
9	<i>Lithothamnium glaciale</i>	99
10	<i>Antithamnion boreale</i>	98

was the umbonal sulcus between the umbone proper and the wings. The phyllodocid polychaete annelids, *Eulalia viridis* and *Eulalia bilineata* were occasionally seen crawling over the surface of either an upper or a lower valve; both species were found to take refuge within empty burrows, especially those left vacant by the boring sponge, *C. vastifica*. Small specimens of the anemone, *Metridium senile*, were found occasionally on an upper valve or very rarely on a lower valve, sometimes with their bases attached in the entrance to an old abandoned burrow; this animal appeared to prefer the umbonal region of the valve, though it was sometimes located in the peripheral region.

Three species of algae were also observed on "live" shells only. These include: the filamentous red algae, *Polysiphonia urceolata* and *Rhodomela confervoides*, both recorded from the peripheral region of the lower valve only; and the blue-green alga, *Entophysalis* sp., which appeared as small, red-coloured patches on the surface of the coralline alga, *Lithothamnium*, growing on upper valves. *Lithothamnium* occurred on preserved shells also.

Special mention should be given to the green sea urchin, *Strongylocentrotus dröbachiensis*, as the only organism found to regularly cause destruction of the epibionts associated with the scallop shell. This echinoid occurs commonly within the study area and has been observed on both upper and lower valves of scallops maintained alive in the laboratory. The animal grazes slowly across the shell surface, its toothed feeding apparatus ("Aristotle's lantern") leaving a characteristic pattern of scrape-marks. It prefers the peripheral and umbonal regions.

There is very little evidence of direct interaction or interdependence amongst the members of this epibiotic association. However, certain observations from the "live" shells should be noted.

What may have been an example of predation was observed on one occasion involving the errant phyllodocid polychaete, *Eulalia viridis*, and the boring spionid polychaete, *Polydora* sp. (specific identification was not possible, due to its seclusion within its burrow). The *E. viridis* was seen wandering over the surface of an upper valve, when it was apparently attracted by the waving movements of the tentacular palps of the *Polydora*, the latter being engaged in normal feeding activity. The *Eulalia* approached the *Polydora* several times over a period of a few minutes, the latter withdrawing momentarily into its burrow each time and then resuming its feeding activity. Finally, the *Eulalia* thrust its anterior end down into the burrow opening and remained there for several seconds; when it withdrew, its proboscis was seen to have been extended considerably. If its object was to capture the *Polydora*, it was unsuccessful.

Another, more puzzling event also involved a specimen of *Polydora*, this time as an apparent predator. A specimen of the nematode, *Anticomma pellucida*, wandered too close to a hydroid polyp (unidentified) and was immobilized, presumably by contact with the latter's nematocysts. This nematode was presented to a large *Polydora* which was feeding from its nearby burrow. The *Polydora* immediately grasped the nematode and withdrew with it into its burrow. Though the burrow entrance was watched for at least ten minutes after this, the *Polydora* did not re-emerge. It is not known whether the nematode was

ingested by the *Polydora*, but such behaviour seems unusual for a deposit/suspension-feeder. It is therefore difficult to understand the reaction of the *Polydora*, and one wonders whether a living, active nematode, wandering too close to a *Polydora* burrow, would be treated similarly.

On another occasion, a tiny specimen of *Polydora websteri* removed alive from a piece of broken scallop shell was presented to a large *Polydora* sp. in its normal feeding position at its burrow entrance; the smaller worm was immediately grasped and taken into the burrow, and was not seen again. This again was puzzling behaviour in view of the normal feeding habits of *Polydora*.

One may assume, from what is generally known of the feeding habits of certain errant polychaetes, that some of these worms which have been observed on "live" shells may occasionally feed upon filamentous algae growing on the shell, as well as upon certain of the associated animals. Apart from this, very little predation of one epibiont upon another would be expected, and none was observed.

At least one free-living animal sometimes reproduces on the scallop shell. A specimen of the polychaete worm, *Eulalia viridis*, was observed leaving an abandoned burrow in a lower valve. After wandering about the surface of the shell near the edge of the valve for about three minutes, the worm paused to deposit a mass of green-coloured eggs which became attached to the shell surface, after which the worm returned to its shelter.

Spatial Dominance

For the 12 scallop shells examined quantitatively, the dominant

species of epibiotic organisms have been determined using data from Table A (Appendix 1). The entire series was first considered as a whole, after which each group (for example, the base group) was treated separately. It was decided that tables of convenient lengths for purposes of comparison would be obtained by including the 10 highest biological index values and their respective species. In a case of similar index values the species involved were awarded equal rank in the scale of dominance. Therefore there occur several ties for single positions of rank, involving either two or three species. The results appear in Table 5.

The top-ranking dominant forms were generally the same throughout the series. *Polydora websteri* and *Lithothamnium glaciale* headed the lists for upper valves, while *Folliculina* sp. was at the first position from the lower valves. The other dominants appeared at various positions of rank according to their relative positions of abundance within each comparison group.

Table 5.1 combines data from upper and lower valves and lists the 10 dominant species from the 12 entire shells. First place is held by the foraminiferan, *Trochammina squamata*, one of the smallest epibionts recorded. Tables 5.2 through 5.11 treat upper and lower valves separately and present dominance information for: (i) the entire series of 12 shells; (ii) the base group; (iii) the "deep water" group; (iv) the "winter" group; and (v) the "young" group.

It should be noted that the maximum possible biological index value within any group depends upon the number of shells included in that group, and so varies from table to table. This causes no problem,

as it is not necessary to compare index values between tables. These indices are compared only within each table, to give the relative ranks.

Several species listed as dominants on upper valves in the base group are of lesser importance in other sub-groups. *Anticoma pellucida*, for example, is a dominant in the base group only. It is rare on the young shells, probably because of a lack of sufficient concealment which is provided by the richer flora and fauna of the older scallops.

Polydora concharum and *Hiatella arctica* are also unrecorded from young shells. The reason in the former case may be due to a relative scarcity of *P. concharum* in the area compared to *P. websteri*, while the latter may find the young shells too smooth for its nestling habits.

Folliculina sp. and *Trochammina squamata* are not dominants on upper valves from deep water. *Folliculina* was less abundant on those upper valves, but this does not seem to be related to depth, as it was very numerous on the lower valves from deep water. The other five dominants from base group upper valves occurred in the corresponding lists for all of the other three sub-groups.

In the lower valves in the base group (Table 5.5) *Folliculina* sp. is the highest ranking dominant species, as a result of its huge numbers on virtually all of the lower valves. Second place is shared by *Cliona* and an ectoproct, *Cribrilina punctata*. Two other ectoprocts, *Nolella* sp. and *Membranipora craticula*, occupy third and fourth positions, respectively, while yet another pair, *Porella aperta* and *Schizoporella auriculata*, rank eighth and ninth. Clearly, ectoprocts account for a great deal of the settlement on lower valves.

This list (Table 5.5) also includes several species which do not

rank as dominants within certain of the other subgroups. *Nolella* is absent from young shells and less common on the two shells-collected in winter. No reason for either case is immediately apparent; and there seems to be no connection, for the young shells were collected in summer. *Porella aperta* was also completely absent from young shells, and occurred in small quantity on only one of the winter shells.

Spirorbis granulatus did not occur on any of the young shells but this was probably due merely to chance, since it has been observed attached to other smooth shell surfaces. The unidentified scyphozoan (scyphistoma stage) is not a dominant in any of the other three sub-groups, and it seems reasonable at least to say that it prefers shallow water in this area. Seasonal occurrence is difficult to specify, as this scyphistoma stage occurred on shells collected both in August and in December.

Trochammina squamata, the foraminiferan which emerges as the over-all dominant species, narrowly missed the lists for the winter-collected and deep-water sub-groups. It was still so numerous on those valves, however, that no season- or depth- related distribution is suggested. The ectoproct, *Schizoporella auriculata*, is absent from the list of dominants for the lower valves from deep water, though it did account for about nine per cent of the area occupied on one of those valves; it was not recorded from the young shells.

As a closing statement on the subject of spatial dominance it may be said that on upper valves a very few species, usually three or four, account for well over 95 per cent of the space occupied on each valve; while the remaining species, numbering from 6 to 22, each make up only a fraction of one per cent. The species at the head of the list

of dominants are nearly always the same, namely: *Polydora websteri*, *Lithothamnium glaciale*, *Dodecaceria concharum*, and *Polydora concharum*.

On the lower valves, the distribution of space amongst the epibionts is more even. There it usually required about a dozen species to make up 95 per cent of the total area occupied. There was considerable variation in the lists of dominants on lower valves, but they generally included *Folliculina* sp., *Cliona vastifica*, and four or five ectoprocts such as *Membranipora craticula* and *Cribrilina punctata*.

Diversity

Two diversity indices have been calculated for the populations associated with the scallop shell surfaces. These are the diversity per individual (unit of area), H , and the evenness, J . Indices were obtained for entire valves and for each region (umbonal, central and peripheral) of each valve.

For entire valves, the values of H are generally low, the highest being 3.62. Lower valves almost always yielded higher H values than did upper valves. Values throughout most of the shell series were fairly uniform except in the case of young shells, where they were much lower. H does not in any case approach closely to its maximum possible value. Low values of J further indicate the uneven manner in which shell surface space is divided amongst the epibiotic species present. These results appear in Table 6, and the diversity indices are also presented graphically in Figure 7.

The diversity indices obtained here for entire valves are fairly uniform (v. Fig. 7), except for those figures calculated for the shells of young scallops (numbers, 8, 9 and 10). The lower values found for

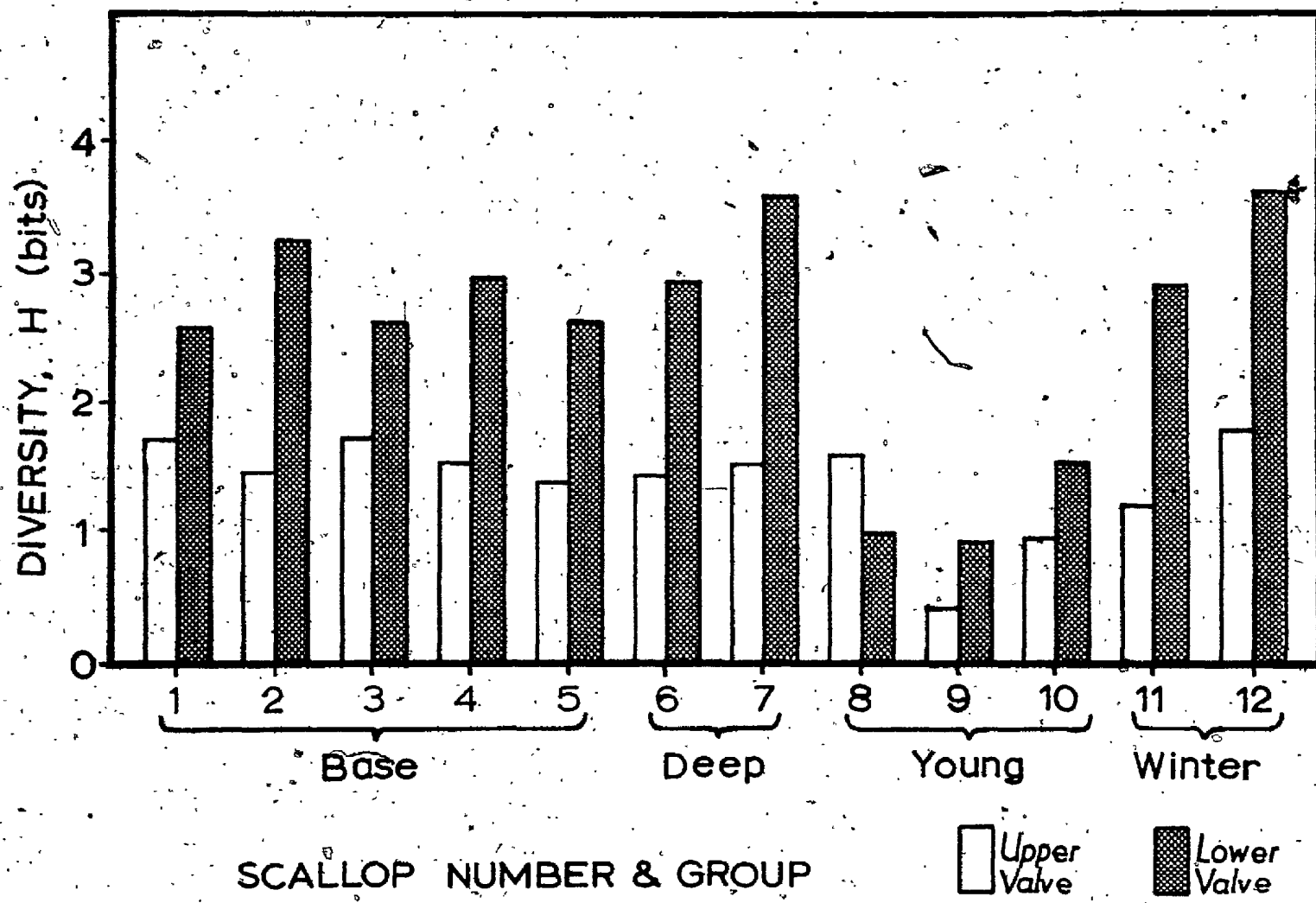
TABLE 6

DIVERSITY INDICES FOR THE EPIBIOTIC ASSOCIATIONS ON THE SHELLS
OF THE 12 SCALLOPS LISTED IN TABLE 2: BY VALVES

Scallop No.	Valve	Diversity per individual, H (bits)	Maximum Possible Diversity per Individual H _{max} (bits)	Evenness, J
1	Upper	1.68	3.32	0.506
	Lower	2.55	4.34	0.588
2	Upper	1.36	2.81	0.485
	Lower	3.18	4.71	0.675
3	Upper	1.69	3.57	0.535
	Lower	2.60	4.86	0.535
4	Upper	1.54	3.58	0.430
	Lower	2.92	4.54	0.643
5	Upper	1.41	3.59	0.393
	Lower	2.72	4.10	0.663
6	Upper	1.45	4.25	0.341
	Lower	2.89	4.85	0.596
7	Upper	1.54	4.17	0.369
	Lower	3.62	4.18	0.700
8	Upper	1.63	2.75	0.593
	Lower	1.02	3.30	0.309
9	Upper	0.359	2.53	0.142
	Lower	0.952	3.72	0.256
10	Upper	0.992	1.56	0.638
	Lower	1.61	2.78	0.579
11	Upper	1.24	4.44	0.279
	Lower	2.96	4.60	0.643
12	Upper	1.77	3.79	0.467
	Lower	3.62	4.98	0.726

FIGURE 7

GRAPH OF DIVERSITY INDICES FOR ENTIRE VALVES OF SCALLOP
SHELLS (DATA TAKEN FROM TABLE 6)



the young shells are no doubt due to the smaller numbers of epibiotic species associated with those shells (v. Tables A.15 to A.20), and would be expected at such an early stage in the development of the association. It would be unwise to attempt to attach statistical significance to these differences, based on such a small group of shells, but the evidence is sufficient to suggest that most young shells in the same age range (2 to 5 years) would give similarly low results. With regard to the other comparison groups, however, there is no evidence to suggest a correlation between either water depth or the season of the year, and the diversity of the shell association.

There is a definite and obvious relationship between upper and lower valves and the diversity indices of their respective associations. With a single exception, all lower valves had higher indices, by at least 50 per cent, than the corresponding upper valves. This exception occurred because, in a situation which was highly unusual for a lower valve, one species (the sponge, *Halisarca* sp.) accounted for more than 80 per cent of the total area occupied. Furthermore, that species and only three others made up more than 98 per cent of the total. The obvious reason for the lower diversity found on upper valves is the highly unequal distribution of shell surface space amongst the species found there, which are fewer in number than the more evenly distributed species on the lower valves. The lowest indices were found on the upper valves having the lowest numbers of species (numbers 9 and 10), while the highest figures belong to those lower valves having the largest numbers of species (numbers 7 and 12). There is no apparent relationship between diversity and number of species with respect to

upper valves. With the lower valves in the "old" age group, however, a fairly consistent pattern of correspondence is evident; but this pattern breaks down when the young lower valves are included.

Further evidence of the unevenness with which occupied space is distributed amongst the occupying species is provided by the low values of evenness, J , appearing in Table 6. Higher values of J in the table correspond generally with higher values of H , but the figures show that H has reached at best only about 70 per cent of its maximum possible value.

Table 7 presents diversity indices by regions. On upper valves, the highest index is usually found in the central region, where the greatest variety of species is found. As would be expected from the usual distribution of organisms, the umbonal region and peripheral region alternate fairly evenly as occupants of second place in the diversity ranking. On lower valves a large proportion of the central region is unavailable for surface occupancy. The umbonal region and peripheral region share about equally in first place ranking. This is rather surprising, since the umbonal region appears on visual examination to be a favourite area for the attachment of a much larger variety of species. This may be only a false impression created by the surface configuration and smaller size of the umbonal region.

Affinities Between Assemblages

The existence of epibiotic populations of organisms associated with each of a series of similar habitats invites comparison of the populations in order to determine whether any similarity exists among them. Such similarity, if present, would result from the recurrence

TABLE 7

DIVERSITY INDICES FOR THE EFIBIOTIC ASSOCIATIONS ON THE SHELLS
OF THE 12 SCALLOPS LISTED IN TABLE 2: BY REGIONS
(U: UMBONAL; C: CENTRAL; P: PERIPHERAL)

Scallop No.	Valve	Region	Diversity per Individual H (bits)	Maximum Possible Diversity per Individual H_{max} (bits)	Evenness, J
1	Upper	U	1.23	2.57	0.479
		C	1.75	2.99	0.585
		P	1.28	2.81	0.456
	Lower	U	1.97	3.12	0.631
		C	0.477	2.22	0.215
		P	2.45	4.10	0.597
2	Upper	U	0.788	1.99	0.396
		C	1.33	2.31	0.575
		P	0.832	2.32	0.359
	Lower	U	2.20	3.61	0.609
		C	1.88	2.79	0.674
		P	3.00	4.65	0.645
3	Upper	U	1.30	2.57	0.506
		C	1.65	3.30	0.500
		P	1.47	3.58	0.410
	Lower	U	2.35	4.00	0.588
		C	1.44	2.42	0.594
		P	2.47	4.60	0.537
4	Upper	U	0.980	2.31	0.424
		C	1.54	3.43	0.449
		P	0.727	3.30	0.220
	Lower	U	2.22	3.83	0.580
		C	1.70	2.80	0.606
		P	2.83	4.25	0.666

TABLE 7 (CONTINUED)

Scallop No.	Valve	Region	Diversity per Individual H (bits)	Maximum Possible Diversity per Individual H _{max} (bits)	Evenness, J
5	Upper	U	1.30	2.97	0.438
		C	0.912	2.31	0.394
		P	1.01	3.27	0.319
	Lower	U	2.60	3.68	0.707
		C	0.535	0.929	0.576
		P	2.04	3.39	0.602
6	Upper	U	0.813	3.44	0.236
		C	1.47	3.32	0.443
		P	1.39	3.89	0.357
	Lower	U	1.82	3.59	0.507
		C	0.595	1.89	0.315
		P	2.83	4.78	0.592
7	Upper	U	0.962	3.58	0.270
		C	1.67	3.44	0.485
		P	1.20	3.68	0.326
	Lower	U	2.96	4.46	0.664
		C	1.92	3.50	0.549
		P	2.89	4.96	0.583
8	Upper	U	0.311	1.94	0.160
		C	(nothing present)	(nothing present)	(nothing present)
		P	0.938	1.55	0.605
	Lower	U	1.15	2.51	0.458
		C	1.17	2.30	0.508
		P	0.751	3.16	0.238

TABLE 7 (CONTINUED)

Scallop No.	Valve	Region	Diversity per Individual H (bits)	Maximum Possible Diversity per Individual H _{max} (bits)	Evenness, J
9	Upper	U	0.0332	1.94	0.0171
		C	0.567	1.53	0.370
		P	0.264	1.43	0.185
	Lower	U	0.842	2.17	0.388
		C	-0.000000736	-0.000242	0.00305
		P	0.961	3.49	0.275
10	Upper	U	-0.00000363	-0.720	0.00000505
		C	0.749	1.26	0.596
		P	0.0	0.0	0.0
	Lower	U	1.53	2.32	0.655
		C	0.00363	0.822	0.00442
		P	0.696	1.68	0.414
11	Upper	U	0.494	3.45	0.143
		C	1.09	3.58	0.305
		P	1.08	3.87	0.279
	Lower	U	2.80	4.00	0.700
		C	1.29	2.66	0.486
		P	2.60	4.28	0.607
12	Upper	U	1.52	3.15	0.483
		C	0.966	3.29	0.294
		P	0.987	3.13	0.315
	Lower	U	3.40	4.26	0.799
		C	2.34	3.68	0.636
		P	3.20	4.63	0.691

of groups of species, in similar proportions, from one population to another. The degree of similarity between the members of a pair of populations can be measured by calculating an index of affinity between the two populations. The value of this index is used as the basis for a decision whether the populations are essentially the same with respect to their species compositions and proportions. Indices are similarly calculated for all possible pairs of populations under study and, if the results are sufficiently high, the worker may decide that there is a regular (and now predictable) community of epibiotic organisms to be found in association with that particular habitat within his study area.

The minimum value of the index of affinity on which a positive decision will be based must be decided somewhat arbitrarily in advance by the researcher, after examining the results of previous workers. McCloskey (1969), on the basis of the methods and results of earlier investigators, regards an index of 36.0 as low, but still high enough to indicate the existence of a community; the value 23.35 was rejected as too low. A reasonable minimum value would therefore lie somewhere not too far below 36.0, yet above 23.35. At the beginning of this study, a value of 30.0 was chosen as a minimum index.

Comparisons of upper valve *versus* lower valve (intra-scallop only), shown in Table 8, indicate that their associations are generally not very similar. Nine of the twelve indices were well below the minimum of 30.0. One of the other values, 32.6, barely qualifies and even the highest figure, 46.2, is still not very high. The average of the 12 indices is 12.8, which clearly indicates that the associations

TABLE 8

COMPARISON OF EPIBIOTIC ASSOCIATIONS: INTRA-SCALLOP, BY VALVES
(UPPER *VERSUS* LOWER). SCALLOPS NUMBERED 1 THROUGH 12,
AS LISTED IN TABLE 2

Scallop Number	Number of Species Common to Upper and Lower Valves	Index of Affinity between Upper and Lower Valves
1	5	41.6
2	4	16.4
3	7	0.0656
4	5	2.34
5	5	32.6
6	12	2.22
7	16	3.12
8	4	2.38
9	4	0.363
10	4	46.2
11	14	3.45
12	10	2.63

on upper and lower valves are not parts of the same community.

Inter-scallop comparisons produced quite different results. Because of the difference between the associations on upper and lower valves, as already indicated by the studies of species composition, dominance and diversity, it was decided here to compare upper valves with other upper valves only, and lower valves only with lower valves. The results (Tables 9.1 through 9.4 and Table 10) indicate that on the "old" scallops (aged 10 to 14 years) there is a high degree of similarity among the associations on upper valves and much less similarity among lower valves. In both cases the indices varied considerably, as can be seen from the ranges given in Table 10. For the upper valves all values exceed the minimum for a community and the average values range from 74.9 to 78.9. In the case of the lower valves, however, many indices lie below the minimum and even the highest values are below the averages of the upper valves. But when the average values for the lower valves are considered (range: 32.9 to 41.5), they are seen to lie above the minimum in each case. Since each is the average of ten pair-comparisons, it is felt that they together constitute a sufficient basis upon which to base a positive decision with regard to the existence of a community associated with the lower valves. It may be stated, therefore, on the basis of these results, that a regular community exists in association with the scallop shells from the present study area. This community has two separate components, the upper valve community and the lower valve community. The two communities are not the same, though they share a number of species. Each has its own dominant species, a few of which

TABLE 9.1

COMPARISON OF EPIBIOTIC ASSOCIATIONS: INTER-SCALLOP, BY VALVES.
 BASE GROUP OF 5 SCALLOPS ("OLD"/SUMMER/6 METERS),
 NUMBERED 1 THROUGH 5.

Scallop No. vs. Scallop No.		Index of Affinity	
		Upper Valves	Lower Valves
1	2	71.7	17.9
1	3	80.9	20.8
1	4	79.3	28.3
1	5	78.2	60.2
2	3	69.5	44.0
2	4	87.7	38.5
2	5	88.7	29.6
3	4	76.2	52.3
3	5	68.7	14.4
4	5	88.4	22.8

TABLE 9.2

COMPARISON OF EPIBIOTIC ASSOCIATIONS: INTER-SCALLOP, BY VALVES.
 BASE GROUP (NUMBERS 1 TO 5) *VERSUS* 2 SCALLOPS
 (NUMBERS 6 AND 7) FROM LOWER DEPTH (20 m)

Scallop No. vs. Scallop No.		Index of Affinity	
		Upper Valves	Lower Valves
6	1	89.2	40.4
6	2	76.6	41.2
6	3	72.2	55.9
6	4	82.9	68.7
6	5	83.3	32.5
7	1	91.6	11.3
7	2	71.5	28.9
7	3	74.5	20.5
7	4	79.3	22.7
7	5	48.6	20.1

TABLE 9.3

COMPARISON OF EPIBIOTIC ASSOCIATIONS: INTER-SCALLOP, BY VALVES.
 BASE GROUP (NUMBERS 1 TO 5) *VERSUS* 2 SCALLOPS
 (NUMBERS 11 AND 12) TAKEN IN WINTER

Scallop No. vs. Scallop No.		Index of Affinity	
		Upper Valves	Lower Valves
11	1	79.6	24.7
11	2	62.0	65.9
11	3	62.7	52.9
11	4	66.4	53.1
11	5	70.3	35.6
12	1	93.6	19.3
12	2	74.2	41.7
12	3	77.0	45.1
12	4	80.2	55.8
12	5	83.4	21.2

TABLE 9.4

COMPARISON OF EPIBIOTIC ASSOCIATIONS: INTER-SCALLOP, BY VALVES.
 BASE GROUP (NUMBERS 1 TO 5) *VERSUS* 3 YOUNG
 SCALLOPS (NUMBERS 8, 9 AND 10)

Scallop No. vs. Scallop No.		Index of Affinity	
		Upper Valves	Lower Valves
8	1	87.1	13.0
8	2	59.3	15.6
8	3	75.5	16.5
8	4	71.3	16.7
8	5	65.5	7.03
9	1	44.5	12.1
9	2	26.5	20.0
9	3	27.7	19.0
9	4	30.4	27.3
9	5	35.2	5.61
10	1	30.5	11.0
10	2	21.1	18.1
10	3	22.3	22.0
10	4	25.0	25.0
10	5	29.8	4.8

TABLE 10

AVERAGE INDICES OF AFFINITY, CALCULATED
FROM DATA IN TABLES 8 AND 9

Groups Compared	Valve	Average Index of Affinity	Range of Values
"Base" Group (inter-scallop comparison)	Upper	78.9	68.7 -88.7
	Lower	32.9	14.4 -60.2
"Base" Group (intra-scallop comparison)	Upper vs.		
	Lower	12.8	0.0656-46.2
"Base" vs. "Deep Water"	Upper	77.0	48.6 -91.6
	Lower	34.2	11.3 -68.7
"Base" vs. "Winter"	Upper	74.9	62.0 -93.6
	Lower	41.5	19.3 -65.9
"Base" vs. "Young" Scallops (Nos. 8, 9 & 10)	Upper: No. 8	71.7	59.3 -87.1
	" : No. 9	32.9	26.5 -44.5
	" : No. 10	25.7	21.1 -30.5
	" : All 3	43.4	21.1 -87.1
	Lower: No. 8	13.8	7.03 -16.7
	" : No. 9	16.8	5.61 -27.3
	" : No. 10	16.3	4.80 -25.4
	" : All 3	15.6	4.80 -27.3

are also occasionally shared. The composition of the lower valve community is considerably more variable and, hence, less predictable.

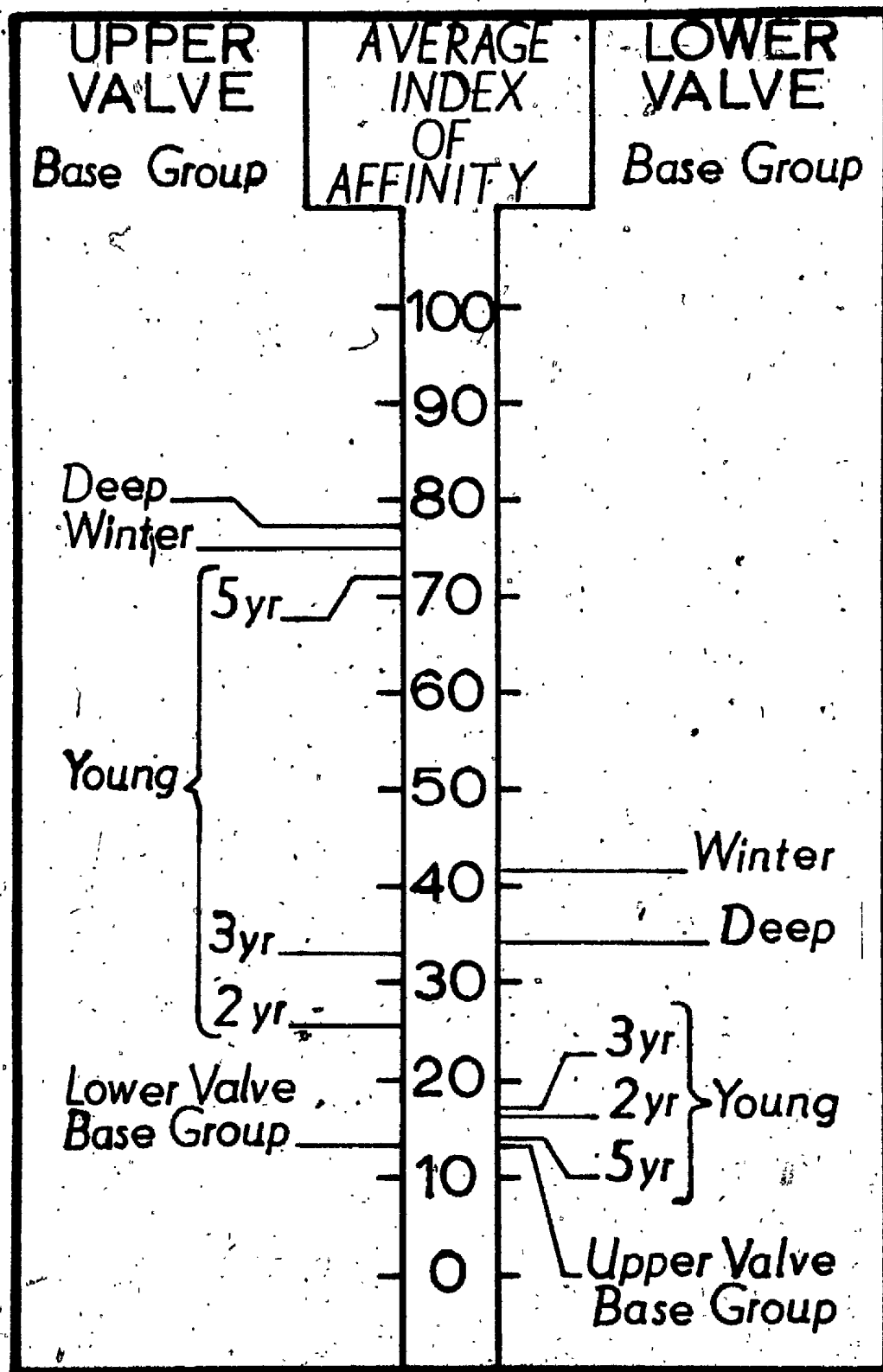
There is no evidence of any change in the general species compositions of the upper and lower valves, respectively, when observed at the lower depth or in the winter season. The indices obtained from the three inter-group comparisons lie very close together, as can be seen from the averages and ranges. (Table 10 and Figure 8).

The results of the comparison between the base group and the group of young shells are much less uniform. These young shells were two, three and five years of age, respectively, and the indices obtained from the upper valve comparisons with each produced averages so far apart that an attempt to consider a realistic average for the whole group is certainly pointless. The averages do, however, indicate a trend. With respect to the upper valves only, the similarity between the base group and the young group increases as the young scallop gets older. The index for the five-year-old scallop is definitely high enough to consider that it shares the same community with the older upper valves. The index for the two-year-old is certainly too low, while that for the three-year-old is just above the minimum. The upper valve community, then, seems to become established somewhere between the (scallop's) ages of two and five years.

For the lower valves, all average indices are about the same, and are very low. Even on the five-year-old shell, the lower valve association is very dissimilar to the community on the old lower valves. It is not possible to say, on the basis of these results alone, at which shell age the typical lower valve community reaches full development.

FIGURE 8

RELATIVE SIMILARITIES BETWEEN EPIBIOTIC COMMUNITIES ON SHELLS IN
BASE GROUP AND OTHER COMPARISON GROUPS, AS SHOWN BY AVERAGE
VALUES OF INDICES OF AFFINITY (DATA FROM TABLE 10)



It would be reasonable to expect it to take longer than the upper valve community, in view of the greater degree of variability already seen to be inherent in it. To be certain, it would be necessary to study scallops between the ages of five and ten years, which would probably be as difficult to locate as were the younger ones included here.

Within each valve, inter-regional comparisons of associated populations were made, in order to determine the validity of these arbitrarily-chosen regions as distinct segments of the valve community. Here, again, the results (Table 11) varied considerably. On the upper valves, the comparatively high degree of similarity, shown by the average indices (all above the minimum), indicate that the regions support essentially the same communities and are therefore not valid ecologically. The indices for the lower valves are slightly smaller, but two averages are only a little below the minimum and one is well above it. The same conclusion should therefore be made: the regions are not valid with respect to their epibiotic associations on the lower valve, either. However, the regions are still useful for convenient sub-division of the surface of the shell and are probably as good as any other system, for that purpose.

Fidelity, Vitality and Periodicity

Having listed the epibiotic species found associated with the scallop shell, and having determined the dominant forms in the community, it seems appropriate here to say something about the degree to which these epibionts are peculiar to the environment of the scallop shell. This may be considered in terms of the concepts of fidelity, vitality and periodicity, the last of which is self-explanatory.

TABLE 11

COMPARISON OF EPIBIOTIC ASSOCIATIONS: INTRA-SCALLOP, BY REGIONS.
(U: UMBONAL; C: CENTRAL; P: PERIPHERAL)

Scallop No.	Index of Affinity					
	Upper Valve			Lower Valve		
	U vs. C	U vs. P	C vs. P	U vs. C	U vs. P	C vs. P
1	67.2	37.1	65.7	15.5	56.2	2.32
2	26.0	20.2	82.3	34.0	35.6	39.3
3	55.4	43.4	88.0	32.7	59.9	15.8
4	32.8	22.7	77.4	28.3	47.3	55.8
5	31.5	36.3	31.8	24.4	37.3	27.6
6	12.6	13.6	89.5	56.6	40.5	24.3
7	58.5	46.3	83.2	8.14	9.59	6.74
8	0.00	0.00	0.00	46.8	18.1	69.9
9	7.19	94.7	7.41	81.9	89.5	77.6
10	0.00	100	0.00	10.0	30.7	10.1
11	80.1	30.7	49.8	33.3	43.9	16.7
12	27.0	24.5	87.8	34.2	45.2	46.3
Mean: (less No.s 8, 9, 10)	43.4	30.5	72.8	29.6	41.7	26.1

Fidelity is the degree to which a species is restricted to the assemblage under study, while vitality is an indication of the completeness of the species' life cycle within the assemblage. In some cases the fidelity of the species can be stated in general terms only, because the species and its ecology are imperfectly known, and the organism may well occur in habitats which have not yet been investigated. However, it appears reasonable to state that none of the species occupying the first ten positions of dominance on each valve are found only on scallop shells. In fact, most are generally known to occupy other suitable substrates.

Table 12 summarizes what may be said with reasonable certainty regarding the fidelity, vitality and periodicity of 16 dominant species from the 24 valves. Also in the table, the animals are classified as to general feeding type.

TABLE 12

FIDELITY, VITALITY, PERIODICITY AND FEEDING TYPE (OF ANIMALS) FOR DOMINANT SPECIES
IN THE *PLACOPECTEN* COMMUNITY. SPECIES ARE RANKED BY THEIR BIOLOGICAL INDEX
VALUES, IN THE ORDER IN WHICH THEY APPEAR IN TABLES 5.2 AND 5.3

Species	Fidelity	Vitality	Periodicity	Feeding Type
<i>Lithothamnium glaciale</i>	Common on other substrates, e.g., rocks, shells of molluscs.	Complete life cycle within the community.	None.	-
<i>Polydora websteri</i>	Common in shells of other molluscs.	Breeds within the community; larvae are planktonic.	None.	Suspension- / deposit- feeder.
<i>Trochammina squamata</i>	Common on other benthic substrates.	Complete life cycle within the community.	None.	Deposit-feeder.
<i>Dodecaceria concharum</i>	Common in other calcium carbonate substrates.	Breeds within the community; larvae are planktonic.	None.	Suspension- / deposit- feeder.
<i>Polydora concharum</i>	Common in shells of other molluscs.	Breeds within the community; larvae are planktonic.	None.	Suspension- / deposit- feeder.
<i>Cliona vastifica</i>	Common in other calcium carbonate substrates.	Complete life cycle within the community.	None.	Filter-feeder.

TABLE 12 (CONTINUED)

Species	Fidelity	Vitality	Periodicity	Feeding Type
<i>Eggerella advena</i>	Common on other benthic substrates.	Complete life cycle within the community.	None.	Deposit-feeder.
<i>Folliculina</i> sp.	Common on other benthic substrates.	Complete life cycle within the community.	None.	Suspension-feeder.
<i>Hiatella arctica</i>	Common borer in shells, rock, etc.	Breeds within the community; larvae are planktonic.	None.	Filter-feeder.
<i>Anticoma pellucida</i>	Common in many other marine habitats.	Complete life cycle within the community.	Much less abundant in winter.	Carnivore (?) Deposit-feeder(?)
<i>Membranipora craticula</i>	Common on many other firm substrates.	Breeds within the community; larvae are planktonic.	None.	Filter-feeder.
<i>Gribrilina punctata</i>	Common on many other firm substrates.	Breeds within the community; larvae are planktonic.	None.	Filter-feeder.
<i>Antithamnion boreale</i>	Common on other shells, stones, etc.	Complete life cycle within the community.	None.	-

TABLE 12 (CONTINUED)

Species	Fidelity	Vitality	Periodicity	Feeding Type
<i>Spirorbis granulatus</i>	Found on other firm substrates.	Breeds within the community; larvae are planktonic.	None.	Filter-feeder.
<i>Spirorbis spirillum</i>	Common on many other substrates.	Breeds within the community; larvae are planktonic.	None.	Filter-feeder.
<i>Nolella</i> sp.	Common on many other substrates.	Breeds within the community; larvae are planktonic.	Not recorded in winter.	Filter-feeder.

DISCUSSION

The shells of the sea scallop from Salmonier Arm support an interesting and varied fauna and flora. This shell is an eminently suitable subject for a study of a semi-isolated ecosystem. Resting as it does upon a sea bottom of mud and sand, its calcareous structure creates an environmental substrate greatly different from its surroundings. It is of easily manageable size and capable of being examined in its entirety. As a totally lifeless substrate, the shell in itself exerts no active influence upon the organisms attached to or resting upon and within it (though the living scallop within the shell may have some effect, as will be seen later). It occurs year-round over a wide range of depths, making it ideal for a study of season- and depth-related variations. In addition to a great abundance of adult scallops within the area, it is also possible (though with some difficulty) to obtain young specimens, whose shells demonstrate the early stages in the development of the association.

The Scallop Shell Surface: Natural History

Hedgpeth (1957) states: "Because of the great volume of the oceans, the quantity of particulate matter carried in suspension is immense, and this quantity makes possible the enormous variety and numbers of organisms adapted to feed upon such material. Such filter- or suspension feeding organisms make up most of the epifauna and infauna of sea bottoms." The shell of the scallop in Salmonier Arm provides a suitable substrate for some of this epifauna (and epiflora), both permanently-attached forms and others which have some degree of

mobility and may be only occasional visitors to the shell.

Of the 74 recorded species, 46 are sessile forms, being permanently attached to the shell for the duration of their lives. Eight others lead a sedentary existence, staying at the same location for very long periods of time and in some cases temporarily attached to the surface. The remaining 20 species are free-living and, presumably, move about the shell surface. Some of these, such as the errant polychaetes, are quite active while others, like the foraminiferans, seem to remain stationary for longer periods.

The scallop does not appear to suffer any harm or disadvantage from the presence of these associates on or in its shell. Many of the epibionts probably do not require the presence of the live scallop within the shell. Powell (1968) reported that bryozoans were particularly common encrusting the internal surfaces of disarticulated valves of *Placopecten magellanicus* which had apparently been thrown back into the sea (Bay of Fundy, Nova Scotia) after having been shucked by fishermen; he found only a very few cases of colonies encrusting live scallops. In his review publication, Cheng (1967) discusses the status of several common types of associates often found on or in molluscan shells. None of the boring sponges, he states, is believed to be a true parasite; where they occur in oyster shells, for example, they ". . . do not draw their nutrients from the body of the oyster". The tunnels excavated by the sponge, he continues, do not usually perforate the inner surface of the shell, except occasionally in the case of old and heavy infestations, in which case the perforations are usually mended by deposition of new shell material. Cheng says also

that most of the cnidarians known to be associated with marine molluscs are simply "epiphoronts". Of the annelids, Cheng says that it is believed that the members of the genus *Polydora* are definitely not parasites. Finally, there is no reason to suspect that the presence of the epibionts would impair the normal functioning of the shell, except perhaps in a rare case of an unusually severe infestation of *Ciona* in the immediate vicinity of the hinge, the possibility of which was mentioned earlier, under Results and Observations.

It is necessary to try to understand the reasons for the existence of the association and the nature of the relationships between the associates and their environmental substrate. Most of the animals encountered here and, of course, all of the plants studied, live a sessile or sedentary life. Such a mode of existence requires a firm or solid substrate, according to the particular needs of each species. In those animals whose life cycle includes a pelagic larval stage, the larvae must locate a suitable substrate at the appropriate time near the end of its pelagic existence and just prior to settling. The sea bottom within the study area consists of mud and sand, with rocks occurring very infrequently. The scallop shells provide virtually the only areas of suitable substrate upon which larvae may safely settle and undergo metamorphosis. Similarly, the shells provide the necessary firm footing for the algae occurring in the area. Established at distances of up to three or four centimeters above the sea bottom, the organisms are able to feed, grow and reproduce, free from the danger of being dislodged from their sites of attachment or buried under mud or loose sand.

Is this situation any different, then, from the simple fouling of any firm surface which is constantly immersed in the water? The

scallop does not seem to benefit from having the organisms associated with its shell, but neither does it appear to be harmed. The associates do not, at first glance, seem to gain any advantage that they would not have if attached instead to a rock, a wharf piling, or even to an empty shell. However, there are two possible advantages to the epibionts on the scallop shells, which are not immediately apparent. A completely inert substrate situated close to a muddy sea bottom may be subjected periodically to silting caused by material stirred up by water currents. This could prove disastrous to a sessile animal if the silting should continue indefinitely without relief. A living scallop would not permit itself to be covered in, but would rapidly open and close its valves, thus dislodging the mud or sand. This, together with lesser, more normal movements of the shell, would keep the surfaces of the valves relatively free of silt.

Also, Cheng (1967) quotes various workers who believe that animals occurring on the outer surfaces of the shells of marine molluscs may derive some benefit from the faeces, pseudofaeces and mantle fluids introduced into their environment by the pumping activity of the animal on whose shell they are living. There is also the possibility that water currents created by the host mollusc in its own feeding behaviour may carry suspended food material close to the shell surface where it may become more accessible to filter-feeding epibionts. Cheng found no record of a true parasite having been reported from the external surface of the shell of any marine mollusc.

Empty shells of *P. magellanicus* have also been observed to support associations of living organisms. No investigation of this

phenomenon has been included in this study, but it has been noticed that disarticulated scallop shell valves lying in trays of running sea water in the laboratory always bore fouling organisms not only on their external surfaces, but frequently on their internal surfaces as well.

As already mentioned, Powell (1968) observed fouling on the internal surfaces of empty scallop shells in the Bay of Fundy. Similarly, some of the epibionts listed in this paper have been seen by the author during casual inspection of empty shells included unintentionally in mass collections from Salmonier Arm. Such associations attached to disarticulated shells could survive only as long as the shells remained free from heavy silting. Given the bottom characteristics in the area, as already described (loose sand and mud), such silting might occur fairly frequently.

Evans' (1969) x-radiographic study of borers involved disarticulated sea scallop valves held for a period of six months in wire cages suspended in the ocean. All borers exhibited growth during that time. Evans also observed an unusual phenomenon in certain of the empty lower valves. Specimens of *Polydora* sp. had settled and begun to grow in *Cliona* burrows. He suggested that these particular lower valves had been replaced in the cages with their external surface uppermost, following one of the periodic examinations. This indicates that preferential choice of upper valves for settlement by *Polydora* may be related to some factor or factors other than the characteristic surface of the upper valve. Whether this factor is light intensity, gravitational force or something else remains to be demonstrated.

What are some of the factors involved in the recruitment and settlement of new members in this association? Most of the organisms

recorded are sessile or sedentary forms, depending for their dispersal upon their larval stages, which must survive the rigours of changing temperature and salinity, obtain sufficient food, escape predators, and locate within a certain period of time a suitable substrate on which to settle. Little is known of the temperature and salinity tolerances of most of the epibionts, and physical data from the area are not really extensive enough to be used as the basis of a detailed study of this sort. It has been noted, however, that the salinity values available are rather low (see Materials and Methods), and the occupants of the shells must be capable of living under such conditions. Hopkins (1956) has reported that *Cliona vastifica* is commonly found under estuarine conditions in the Gulf of Mexico, and that it can in fact survive periods of nearly fresh water; other *Cliona* species require high salinities.

Light is also an important factor in the settlement of marine larvae. Thorson (1964) brought together data previously reported for 144 species; in their early pelagic stages only 12 per cent of these appeared to be indifferent to light; most (82 per cent) were photopositive. In their later and oldest pelagic stages most of the initially photopositive larvae became photonegative and sought deeper water. When encountering the scallop shell, some of the larvae probably seek the shaded lower valve; besides *Cliona*, these would include most of the ectoprocts, the surface-dwelling sponges and most of the ascidians, which are rarely found on an upper valve. Others, such as *Polydora*, *Dodecaceria* and some of the rare species, prefer the upper, better-lighted valve. The remainder appear to be indifferent and are commonly

found on both valves. These choices must be made within a limited period of time. This subject is discussed by Thorson (1964), who reports that larvae of *Spirorbis*, most bryozoans and most ascidians have a free-swimming life of only a few hours, and in some cases less than one hour.

The nature of the substratum itself is of great importance to a pelagic larva searching for a firm surface to which it may safely become attached. A single scallop shell is a very small target when compared with the area of the sea bottom within the study area. Although some larvae are able to postpone their settling time for several days or more (Thorson, 1966), this extension is limited and the time eventually arrives when the larva must settle. Those larvae which fail to pass over a scallop shell within their time limit are forced to settle on the silty bottom and soon die. This chance arrival of each of the many larval species in the water overlying any particular scallop shell at the precise time at which they are due to settle no doubt accounts for much of the variation observed in the epibiotic associations on the shells examined.

Mention has already been made, in the Results and Observations section, of the destruction of parts of the epibiotic association by the sea urchin, *Strongylocentrotus dröbachiensis*. This is the only recorded member of this shell association capable of mass destruction of other epibionts. An area of shell surface grazed by an urchin would probably be resettled fairly quickly by new arrivals, depending upon the presence of larvae in the water or the growth and spreading of species in areas adjacent to the grazed area. The characteristic marks

left by the urchin might be visible for only a short time, so that the frequency of their occurrence on the shells may be only a small indication of the actual extent of the damage done by this animal. It may well be that *S. dröbachiensis*, which is reportedly numerous in the study area, may cause repeated changes in the species composition of the shell association through the destruction and renewal of certain of its components. It is the upper valve which is more susceptible to such damage, since all the periphery of the lower valve is inaccessible to the urchin because it rests on the sea bottom.

Two animals are conspicuous by their absence from the *P. magellanicus* shell community. The "common mussel", *Mytilus edulis* Linnaeus, and to a lesser extent the "horse mussel", *Modiolus modiolus* (Linnaeus), are very common fouling organisms around the shores of the island of Newfoundland. Sergy (1972) reported *M. edulis* as one of the two most abundant foulers of Logy Bay (the other was *Hiatella arctica*). John W. Evans (personal communication) states that mytilids were greatest in numerical importance in recent (1972) studies of larval settlement at Garden Cove, Placentia Bay (which lies next to St. Mary's Bay on the same coast). Due to the small size of the larvae, no attempt was made to distinguish between *Mytilus* and *Modiolus*. Second in importance once again was *Hiatella*. Five different test substrates were equally favoured by the mytilids. The density of the mytilid settlement decreased with increasing depth, but at 21 meters the mytilids were still second in numerical importance (after *Anomia* sp.) at the time of heaviest general larval settlement (September).

In view of the common occurrence of mytilids on various substrates

in nearby areas, as just described, it is difficult to explain their absence from the scallop shells in Salmonier Arm on the basis of physical characteristics of the environment alone. Instead, it may be that the mytilids are repelled by a substance or substances secreted by the scallop. Cheng (1967) proposes that chemotaxis involving substances secreted by the host may be factor in the attraction of symbionts to molluscan shells, but admits that only suggestive evidence of this exists. If this is so, then there might also be other chemicals which would repel certain larvae. Such a chemical factor would not, of course, keep mytilids away from empty, disarticulated shells. A further study of this phenomenon would require the examination of a large number of empty shells from within the study area, in order to establish the presence or absence of mytilids.

Species Present

Scott (1968) conducted a preliminary survey of the epifauna of the shell of *Placopecten magellanicus* collected from the same general area in Salmonier Arm. She recorded 45 forms, most of which were encountered during the present study. In the light of taxonomic studies carried out by certain specialists and by the author, several of Scott's identifications appear rather doubtful. The hydroid identified as *Stauridia* sp. was probably *Stauridiosarsia producta*, which was recorded in this study from nearly all parts of the shell. The juvenile barnacle described by Scott as tiny and nearly transparent and identified as *Balanus crenatus* has been examined by Dr. E. L. Bousfield and designated as *Balanus* sp., probably *B. balanus*. The encrusting bryozoan (Ectoprocta) described and illustrated by Scott and called *Microporella* sp., is, in fact,

Cylindroporella tubulosa. And the colonial ascidian (Genus *Didemnum*) which bears white stellate spicules is not *D. candidum*, which has a more southerly range (Dr. N. J. Bernikf, personal communication), but is instead *D. albidum*. The remainder of Scott's (1968) identifications appear to be valid. The larger number of forms (74) recorded in the present study is believed to be due to the longer period of time available, resulting in a more thorough examination of the shells.

Merrill (1961) discussed the association of organisms found on upper valves only of *P. magellanicus* (locality not stated, but believed to be Woods Hole, Massachusetts). Only an abstract is available, based on a paper delivered at a scientific meeting. No species list was included, but the most common associates (called "commensal species" by Merrill) were a boring sponge, *Cliona celata*, sea anemones, and bryozoans, both branching and encrusting. Merrill viewed the association as "simply a fouling community", stating that the organisms were to be found on other suitable substrates in the vicinity. The same might be said of most of the associates of the scallop shell in Salmonier Arm, but factors other than the mere presence of the same species elsewhere must be taken into consideration when evaluating a fouling association. The question of the distribution of species, and their abundance and frequency of occurrence, is also important.

It is interesting to note that Merrill described *Cliona celata* as forming large irregular masses 8 to 10 inches high over the surface of the shell, as well as boring into the shell. No such surface growth was observed in *Cliona vastifica* in this study.

Caddy and Chandler (1968) reported only 13 forms associated directly with shells of *P. magellanicus* in the Bay of Fundy, Nova Scotia.

Forms which seem to be similar to those found on Salmonier Arm scallops include: *Cliona* sp., *Spirorbis* sp., *Balanus balanus*, *Anomia* sp., and *Hiatella arctica*. The investigation was a preliminary one and details of the faunal analysis have not yet been published (J. F. Caddy, personal communication), but the faunal list seems unusually short. It may be that some of the smaller forms were missed in that brief survey.

A study of the benthic epifauna in an area of the Clyde Sea, Scotland (Allen, 1953) included an examination of the shells of the scallop, *Chlamys septemradiata*. Once again the species list was short. Only 14 forms were reported, all of which (except a single specimen of *Hiatella arctica*) occurred only on upper valves, which is surprising in view of the diverse fauna observed on lower valves of the sea scallops in Salmonier Arm.

The most interesting epifauna of a scallop other than *P. magellanicus* was that reported by Wells, Wells and Gray (1964), associated with the calico scallop, *Aequipecten gibbus*, from an off-shore bank in North Carolina. Of 112 forms listed as occurring on the shells of living calico scallops, only three were encountered on the sea scallops in this study. They are *Polydora websteri*, *Anomia simplex*, and *Hiatella arctica*. The comparatively large number of associates is believed to reflect the more southerly latitude of that study area, with its higher temperatures, though other less obvious factors may also be involved.

Korringa (1951) recorded 136 forms from Dutch oyster (*Ostrea edulis*) beds. All of these except certain of the polychaete worms were

found on shells of living oysters. Species common to the present study were: *Dodecaceria concharum*, *Eulalia viridis*, *Cirratulus cirratus* and *Phyllodoce maculata*. Related species included: *Cliona* (*Clione*) *celata*, *Haliclona* (*Haliclone*) *limbata*, *Aurelia aurita* scyphistoma, *Polydora ciliata* and *P. hoplura*, and *Folliculina ampulla*. The latter was actually a catch-all name used to include all species of *Folliculina* present. Korrunga felt that shelter provided by the configuration of the oyster shells was the most important factor in the development of the community.

Wells (1961) listed 303 organisms found on oyster (*Crassostrea virginica*) beds in North Carolina, but did not separately list those which occurred on the shells of living oysters. He did, however, mention those groups most commonly found as associates of the shell. These included: protozoans, most sponges, coelenterates, bryozoans, barnacles and ascidians. All of these groups are represented in the *Placopecten* shell community. Forms found on the oyster beds (including the oyster shells and the intervening areas of sea bottom) include: folliculinids, *Cliona vastifica*, *Halisarca* sp., *Anomia simplex* and *Polydora websteri* and other forms related to epibionts of Salmonier Arm scallops.

McCloskey (1969) performed the first analysis of the faunal community associated with a coral (*Oculina arbuscula*) from locations off North and South Carolina. From eight coral heads he listed 302 species (excluding sponges, colonial forms and plants). Species common to the *Placopecten* community include: *Polydora* sp., *Molgula* sp., *Dodecaceria concharum*, *Spirorbis* spp., *Anomia aculeata* and

A. simplex. The comparatively long species list is probably due in part to the greater number of ecological niches offered by the highly irregular surface of the coral head, as well as to the more southerly latitude.

Dominance

The dominant forms in the *P. magellanicus* shell community have been determined on the basis of occupation of space on the external surface of the shell. Other community studies have also included an examination of the topic of dominance, though the depth of that aspect of the study has varied considerably from author to author.

Scott (1968) made only brief mention of the relative abundance of certain members of the *P. magellanicus* community in her preliminary survey. Merrill's (1961) account of fouling on upper valves of sea scallops states only that the heaviest growth appeared to be due to the boring sponge, *Cliona celata*. No attempt was made to evaluate the relative abundances of the other foulers. Caddy and Chandler (1968) observed that the dominant species associated with sea scallop shells appeared to be the barnacle, *Balanus hameri*, and the brachiopod, *Terebratulina septentrionalis*. In contrast, the barnacle, *Balanus* sp., occurred only infrequently on Salmonier Arm sea scallops, and no brachiopod was recorded. On the scallop, *Chlamys septemradiata*, Allen (1953) stated that the associated species of most frequent occurrence was the foraminiferan, *Crithionina heinckeii*, which occurred in numbers as great as 60 per (upper) valve. One of the dominant species by the standards of the present study was also a foraminiferan, *Trochammina squamata*.

Wells, Wells and Gray (1964) did not perform numerical counts of the associates of the shell of the calico scallop, but they did present a brief analysis of dominance based on density, frequency of occurrence and spatial relations. Dominant forms in the *Aequipecten* community included (in descending order): (i) the barnacle, *Balanus amphitrite*; the polychaete worms, (ii) *Sabellaria floridensis* and (iii) *Pomatoceros caeruleus*; another barnacle, (iv) *Balanus calidus*; and (v) encrusting bryozoans. The bryozoans were most abundant on lower valves, as in the present study. Polychaete annelids and encrusting bryozoans are high on several of the lists of dominants compiled in the present study (v. Table 5).

Wells *et al.* (1964) report that the polychaetes, *Polydora websteri* and *Ceratonereis tridentata*, were found to be the cause of mud blisters on the internal surfaces of the shells of the calico scallop. Although *P. websteri* is a dominant member of the *Placopecten* community, no evidence was found of penetration between the valves of the sea scallop. Both *P. websteri* and *P. concharum* were confined to burrows within the substance of the shell, with burrow openings on the external surface of the shell only.

In the *Ostrea edulis* community described by Korringa (1951), several forms (all described as plankton-feeders) were listed as important members of the association. These were: *Folliculina ampulla*, *Haliclona limbata*, the scyphistoma stage of *Aurelia aurita*, *Polydora ciliata* and *Barentsia gracilis*. Forms closely related to these occupy positions of importance in the *Placopecten* community (v. Table 5).

The "most frequently occurring" species in the *Crassostrea*

virginica community (Wells, 1961) were the polychaetes, *Neanthes succinea* and *Nereis occidentalis*, and the amphipod, *Melita dentata*, indicating a community hierarchy which is considerably different from that associated with *P. magellanicus* (v. Table 5.1). Two high-ranking dominants in the present study, *Polydora websteri* and *Folliculina* sp., occupy sixth and eighth place, respectively, in the list of *C. virginica* community dominants.

Among the dominant forms in McCloskey's (1969) *Oculina arbuscula* community, the first three positions were occupied by: the polychaete, *Syllis gracilis*; a boring pelecypod, *Lithophaga bisulcata*; and *Polydora* sp. Dominance in McCloskey's study was evaluated using a biological index value, by a method similar to that used in this paper. However, McCloskey's index was calculated on the basis of numerical counts of individual organisms, which necessitated the omission of sponges and colonial forms from the study. Important members of the community may have been overlooked in doing so. Sponges (both boring and surface-fouling), bryozoans and ascidians, for example, have been abundant forms in several of the marine communities already discussed (for example, Wells, 1961; and Wells *et al.* 1964). Representatives of those groups are also dominant forms in the *P. magellanicus* community.

However, in spite of the restriction of the numerical data analysis to solitary forms, McCloskey (1969) has obviously carried out a thorough study of a large portion of the coral community. His paper was a valuable reference during the present study.

Diversity

The diversity of an animal or plant association is determined by a combination of factors existing both within the association itself and in the environment. For example, it is well known that associations in polar regions tend to have comparatively low diversity, while tropical assemblages usually have high, or sometimes very high, diversity. Any strong limiting factor, whether biological, physical or chemical, may reduce diversity. This also applies to factors introduced by man, such as pollution; in such cases the number of species is usually reduced while the total number of individuals often remains the same or may even be increased. High productivity can in time lead to interspecific competition for limited space by increasing the number of individuals per species; the diversity is thus reduced (Odum, 1959).

The method used here for the calculation of the diversity per individual, H , uses units of surface area covered, rather than numbers of individuals, in each species. The units of area are chosen arbitrarily (square millimeters were used here), since they appear in both the numerator and the denominator of Brillouin's formula (v. Materials and Methods) and are cancelled out. This formula is free of bias when used for whole communities (Pielou, 1966), as it is here. This is so because it gives an actual determination of the true value of the diversity, rather than an estimate.

The evenness, J , with which the individuals (or, in this case, the total units of area covered) are divided amongst the species in the collection is the ratio between the diversity, H , and the maximum possible diversity, H_{\max} . The maximum possible value of J is therefore

"one", in which case all species present would share equally in the space occupied on the substrate.

The present method for the calculation of diversity by the use of "information content" has been in use only in recent years. Pielou's (1966) paper was the first publication to present a thorough analysis of the various diversity indices and the situations in which each may be properly used. It is therefore risky to compare the various diversity indices published prior to that time. It is also of little value to compare values calculated for different types of collections, even when Pielou's guidelines have been followed, as they require different methods of calculation. Most of the recent diversity studies have involved level-bottom communities in which only samples, rather than entire populations, have been the basis for comparison. However, one study may be mentioned as being comparable to the present work.

McCloskey (1969) examined the fauna associated with the coral, *Oculina arbuscula*, in four areas off North and South Carolina. Entire coral heads, distinct from the surrounding environment, were collected and examined. Animals living both on and within the coral were identified and, as his collections were complete and not samples, McCloskey was able to use Brillouin's formula to calculate the diversity of the fauna associated with each coral head. Unfortunately, McCloskey found it necessary to ignore the plants and all those animals which could not be counted (e.g., colonial species, sponges), which fact may perhaps cast some doubt upon the validity of his diversity results. However, as the situation is somewhat analogous to that of the scallop shell association, a brief comparison is invited.

The diversity indices for entire valves, shown in Table 6, are generally low in comparison with McCloskey's (1969) values for coral heads. Values obtained in this study ranged from 0.359 (for an upper valve) to 3.62 (for a lower valve), while his ranged from 2.73 to 4.96 (approximate values). At least two factors may be cited as possible reasons for this difference. First there is the obvious difference in geographic latitude. In an area much closer to the tropics than is Newfoundland, one would expect to find a greater number of species (McCloskey recorded 302 species, excluding colonial forms, etc.) and hence a more highly diverse fauna. Secondly, the highly irregular surface of the coral, as described by McCloskey, holds numerous tiny pockets filled with silt and mucus. In contrast with the relatively smooth surface of the scallop shell, this provides a more attractive habitat for a wider variety of species.

Borers

The borers within the scallop shells have been examined only in a comparatively superficial manner, with regard to their boring activities. No data analysis has been performed because the data obtained regarding the extent of excavation within the shells were too subjective and too imprecise to permit meaningful statistical analysis. However, the observations made from the radiographic studies (Table 4) are interesting in themselves and shed considerable light on the relative importance of the four species involved.

Members of the genus *Polydora*, whose taxonomy has recently been revised (Blake, 1971) for the east coast of North America, have been reported from many different mollusc shells and other calcareous

substrates. This subject has been well reviewed by Blake and Evans (1973). Under the heading of molluscan infestations, they discuss the three main types of *Polydora* burrows which have been reported: (i) surface fouling; (ii) U-shaped burrows; and (iii) mud blisters on the inner surface of the shell. The only type of burrow encountered in this study was the U-shaped burrow with its opening on the outer surface of the shell. There was no evidence of penetration through the shell or of entrance between the shell and the mantle of the scallop.

The other borer found in virtually every upper valve was *Dodecaceria concharum*. Evans (1969) has reported that this is a boring species which takes over old burrows, such as those of *Polydora websteri*, which have been emptied by the death of the original inhabitant. *D. concharum* proceeds to enlarge the burrow, eventually forming a distinctive burrow of its own. The species therefore occurs in upper valves, where *Polydora* is most numerous. Specimens of *D. concharum* were generally found to be most numerous in the central region, as indicated by the presence of their characteristic burrows, as shown in the radiographs. Umbonal and peripheral regions seemed to be about equally favoured as areas of secondary abundance. In every case but one, the percentage of shell material excavated by *D. concharum* within any region, as well as in the entire shell, was well below that of either *Polydora websteri* or *P. concharum*. In that exceptional case, the abundance of *P. concharum* burrows was well below average level, and *D. concharum* still ranked below *P. websteri*.

In the lower valves the most abundant borer was always the

sponge, *Cliona vastifica*. This is one of a family of boring sponges (Clionidae) which has been reported from a wide variety of calcareous substances. Old (1941) has described the taxonomy and distribution of the Clionidae for the Atlantic coast of North America. Warburton (1958b), in a paper on the species of *Cliona* in eastern Canada, noted that *Cliona vastifica* is common in the shell of *Placopecten magellanicus* off Digby, Nova Scotia, and had also been reported from another scallop, *Chlamys islandicus*, at Hare Bay, Newfoundland.

Evans (1969), commenting on sequence of settlement of borers and distribution of burrows in shells of young *P. magellanicus*, says: "*Cliona vastifica* settles almost exclusively on the lower valve usually in the neighbourhood of the umbone and, to a lesser extent, on a broad peripheral band. No settlement takes place in the center of the lower valve . . . , and only very rarely on the upper valve." The results of this study generally bear out this observation, as well as Evans' statement that *Polydora* and *Cliona* are the first organisms to penetrate the shells of young *Placopecten*. A two-year old shell (No. 10 in the series shown in Table 4) contained no borers at all. In the three-year-old shell (No. 9), the only borers present were *Polydora websteri* in the upper valve and *Cliona vastifica* in the lower valve (umbonal region only). However, the sponge rapidly spreads outward from the sites of its original settlement. In the five-year-old shell (No. 8), *Cliona* burrows were present not only in all three regions of the lower valve, but also in the umbonal region of the upper valve where it had already excavated about 17.5 per cent of the available shell material. In fact, the percentage of the total excavation within that upper valve

due to *Cliona* was nearly double that due to the only other borer, *Polydora websteri*. *Cliona* was found in the upper valves of nine of the twelve shells studied quantitatively, indicating that it commonly spreads across the hinge area from the umbonal region of the lower valve. In seven of these nine upper valves it accounted for the highest percentage of excavation within the umbonal region; and in two cases *Cliona* burrows were also present in the central and peripheral regions. Furthermore, in three of the twelve shells, *Cliona* was the most abundant, in terms of the quantity of shell excavated, of all the borers in the upper valves. So, while it rarely settles on upper valves, this sponge may in time become the most important boring species in some of these upper valves. This fact, together with its undisputed first rank as a borer in lower valves, makes *Cliona vastifica* potentially the most destructive of the four boring species considered here.

Medcof (1949) mentions a boring sponge infesting the sea scallop (*P. magellanicus*) off Digby, Nova Scotia. He does not name it in that paper, but identifies it in a later publication (Medcof and Bourne, 1964) as *Cliona vastifica*. Medcof (1949) describes the site of primary infestation as the area of the umbone on the lower valve. He further states that no evidence of the presence of *C. vastifica* was found in scallops under 8 to 9 years of age (about 4.75 inches diameter), but that the sponge was present in almost all scallops above that size and age. The presence of *C. vastifica* in Salmonier Arm in a scallop only three years old, having a height of only 8.5 cm (3.5 inches) indicates that this sponge attacks *Placopecten* at a much earlier

stage in the scallop's life, in the present study area.

It is important to note the role played by some of the borers in preparing the shell for its invasion by other epibionts. This is referred to in part by Evans (1969) when he classifies the borers as primary and secondary: "Primary borers *Cliona vastifica*, *Polydora websteri* and *P. concharum* settle on a fresh shell surface and proceed to bore". Among his secondary borers, Evans includes *Dodecaceria concharum* which, as already mentioned, settles in old *Polydora* burrows and enlarges them, and the saxicavid bivalve, *Hiatella arctica*, which sometimes nestles in the holes formed in the shell surface by *C. vastifica*. In addition to this, the borers (both primary and secondary) create suitable environmental niches for certain non-boring species. For example, old burrows of various types have been found to harbour such occasional associates as the errant polychaetes, *Eulalia viridis* and *E. bilineata*, or the tube-dwelling worms, *Fabricia sabella* and *Terebella lapidaria*. The grooves adjacent to the entrance to *Polydora* burrows are favourite locations for some of the smaller epibionts such as the foraminiferans, *Trochammina squamata* and *Eggerella advena*, and are sometimes occupied by juvenile specimens of *Hiatella arctica*. The borers are amongst the early species to invade the young scallop shells. By modifying the surface of the shell, they create suitable conditions for the development of the more extensive epibiotic associations which are found on the shells of adult scallops.

Hiatella arctica is included by Evans (1969) in his study of borers, since it is common to find adult specimens within old *C. vastifica* holes. However, as this species also occurs frequently in cracks and

grooves on the surface of the shell, and because of the difficulty often encountered in locating the very shallow *Hiatella* "burrow" in x-radiographs, it was decided here to treat it as a nestling species and include it in the analytical study of the surface organisms.

Evaluation of the Present Study

This study might have been approached in any of several different ways, such as from the point of view of the numbers of organisms present or in terms of biomass. However, a study of numbers would have required the elimination of "uncountable" species such as sponges and colonial forms; and the minuteness of some of the forms recorded would have presented problems in a determination of biomass. Instead, it was decided to take a more elementary approach directly related to the relationship between the epibionts and the surface of the shell on which they live. As mentioned earlier, from the point of view of its possible effect on its neighbours, each species present on a shell is doing two very important things: occupying space on the surface of the shell; and removing food material, either from the substrate or from suspension in the water just above the substrate. The abundance of each species has therefore been measured in terms of its combined influence in these two activities, by assessing its total "area of influence" on the surface of the shell. This method has allowed for the inclusion, within the quantitative aspect of the study, of all species encountered on the shell surface, whether solitary or colonial, and of those boring species which live below the surface but remove food material from it or from the surrounding water.

Every researcher whose investigations reveal a large number of organisms belonging to various phyla faces the problem of the identification of those organisms. Ideally, each species discovered should be thoroughly and correctly identified, in order to lend the greatest possible validity to the work. But this ideal is not always attainable. No single worker can become a specialist in all of the groups with which he may be involved, particularly with those forms which are lesser known taxonomically; and various limitations demand that results be attained within a certain period of time. Despite the use of all available taxonomic keys and the assistance of specialists in areas of particular difficulty, the end result is usually a compromise in which as many as possible of the more important organisms are identified as completely as possible while those of lesser importance may or may not be so thoroughly identified. Such is the case here.

Of the 74 species of epibionts recorded from the scallop shells, 54 (73%) have been identified with reasonable certainty to the species level; 42 of these were identified with the aid of persons regarded as taxonomic specialists. A further 14 (19%) have thus far been identified to the genus level only, 10 of them with the aid of specialists. Finally, 6 (8%) are known only to the level of class, sub-class, order, or sub-order. This uncertainty is regrettable, but it persists only after considerable time and effort have been spent in an effort to complete the identifications. In several cases, the only specimens found were juveniles which even the specialists consulted were hesitant to identify positively.

Other difficulties were also encountered. Due to the limitations

imposed by time and available facilities, and also to human fallibility, some of the associated organisms have undoubtedly been omitted from the study record. Deliberately left out were all forms too small to be detected using a dissecting microscope having a maximum total magnification of approximately 150 X. The smallest solitary organism studied was the foraminiferan, *Trochammina squamata*, which occupied an average area of about 0.01 mm². This method eliminated most of the microfauna such as any bacteria, diatoms, flagellates and amoebae which may have been present. Also, it is possible that some specimens of the smaller meiofaunal species may have been missed, despite great care taken in the methodical examination of the shell surfaces. Finally, a number of tiny free-living forms may have been lost from the shell surfaces during the processes of shucking the scallops and preserving the shells.

The quantitative analysis of the *P. magellanicus* community was preceded by a qualitative examination of approximately three dozen scallops taken from various depths and in different seasons, as described under Materials and Methods. The observations made during that part of the study are, of course, reflected in the description of the natural history of the community. It is felt that this qualitative information is at least equal in importance to the numerical data, in the results of this study.

It is possible, however, that some readers might feel that the value of the numerical data analysis, and hence the value of the results as a whole, may be somewhat limited by the comparatively small number (12) of scallop shells which were studied quantitatively. Such doubts

would be largely unfounded. It is certainly always desirable in any study to include as many samples as possible, but it would be wrong to do so if the thoroughness of the study were to suffer as a result of the limited time available in which to examine each sample. Time might have been saved by merely estimating the abundance of each epibiont, as done by Wells, Wells and Gray (1964), or by raising the lower size limit of the organisms to be considered. But such a superficial study had already been done (Scott, 1968) and it was felt that the present method, involving counting and measuring the epibionts and the use of the widest practical size limits, would produce a more complete picture of the community. The much larger number of species recorded in the present study (74, versus 45 recorded by Scott) would seem to justify the approach taken.

The presence of only two scallops in certain comparison groups (for example, the winter group) may appear to be a disadvantage. But since the base group contains five shells, there are actually 10 comparison-pairs (and hence 10 values) on which to base the index of affinity for that particular comparison. McCloskey (1969) made equally firm decisions based on comparisons of only eight coral heads, and his examination of the fauna was incomplete.

The long time required to thoroughly study a shell of *P. magellanicus* by the present method has already been discussed, but to do any less would be to misrepresent the nature of the community, its species proportions and the distribution of its members.

The *Placopecten magellanicus* Community

The *Placopecten magellanicus* shell community in Salmonier Arm, consisting of separate and distinct communities on upper and lower valves, begins to develop at some time early in the life of the scallop, probably at an age of less than two years. The earliest settlers on the upper valves are probably *Lithothamnium glaciale* and *Folliculina* sp. and on the lower valves, *Folliculina* sp. and *Membranipora craticula*. In the typical community found on shells over ten years old the dominant species are characterized by low fidelity and high vitality, and most are either filter- or deposit- feeders.

The results of the studies involving dominance, diversity and affinity suggest that the community probably undergoes a succession of changes as the shell becomes older and larger and as the members of the community increase in number and size. Certainly, it appears that some of the epibionts, by their presence on the shell, prepare it for invasion by other species at later stages. However, the data here are too discontinuous to permit a proper study of the phenomenon of succession.

In relation to the general benthic ecosystem in Salmonier Arm, the scallop shells fulfil the requirement for a firm, exposed substrate in order that the larvae of certain epifaunal organisms may settle and undergo metamorphosis into the adult form. Rocks and other hard substrates are scarce in the area and most of the animals, as well as the algae, encountered on the shell could not survive on the loose sand and mud which forms most of the sea bottom in the vicinity. Few of the typical infaunal organisms of the area would be at home on the scallop.

shell since its comparatively smooth surface does not generally accumulate significant quantities of silt. Exceptions to this occur in older shells, where mud may sometimes be found inside empty burrows and provide refuge for bottom-dwelling forms.

Future Directions for Research

Now that some of the static characteristics of ecology of the *P. magellanicus* community have been examined in the present study, some thought should perhaps be given to a future study of the dynamics of the associated populations, such as the structure of energy pyramids. Material is plentiful and easily obtainable, and adequate laboratory facilities are available.

The methods used in this study might be used as well to examine *P. magellanicus* shell communities in known scallop beds at other locations in Newfoundland. In particular, knowledge of the *P. magellanicus* shell community in good commercial scallop beds in the Newfoundland area might be useful. Such data might indicate the environmental conditions which are suitable for growth of the sea scallop, and might therefore be used as a guide in the introduction of *P. magellanicus* into new locations in this province.

SUMMARY

1. The shells of twelve specimens of the sea scallop, *Placopecten magellanicus*, collected from St. Mary's Bay, Newfoundland, were examined quantitatively with the objective of describing the assemblage of flora and fauna associated with the scallop. The data obtained were combined with the results of preliminary qualitative studies performed on the shells of approximately three dozen other scallops taken from the same location.

2. The twelve scallops were chosen from within specific collections in order to include shells taken from two different depths (6 m and 20m) and during two different seasons (summer and winter). Nine of the scallops were old adults, aged 10 to 14 years; the other three were young specimens, aged 2 to 5 years.

3. The surfaces of the shells were examined using a stereoscopic dissecting microscope, and the shells were subjected to x-radiography in order to determine the identity of boring organisms. All plants and animals discovered by these methods were included in the study, the lower size limit of these being about 0.01 mm^2 of area. All organisms, both solitary and colonial, were included in the data. The abundance of each species was assessed in terms of space influenced on the shell surface by the area of attachment, the area covered during food-gathering activity, or a combination of these two. Also, all solitary animals were counted.

4. Seventy-four species of epibionts, representing 13 animal and

plant phyla, were discovered and identified as thoroughly as possible. Fifty-three of these occurred on the 12 shells studied quantitatively and are therefore represented by numerical data.

5. The populations associated with the upper and lower valves of the shells, respectively, proved to be distinctly different communities. The lower valve community is more variable in its species composition than is the upper valve community. Some of the epibiotic species are members of both communities, that is, they occur on both upper and lower valves.

6. The frequency and abundance data were used in an analysis of dominance, as well as for the calculation of species diversity based on information content. Diversity indices were generally low (less than 4.00) and were lower for upper valves than for lower valves.

7. The dominant species are sessile or sedentary in habit and are either filter- or deposit- feeders. They are not obligate members of the community, but are known to occur in other habitats. However, they reproduce and in some cases complete their entire life cycle within the community.

8. The associations on the youngest shells differed considerably in species composition and in diversity from the typical community. The upper valve community appears to be established by the time the scallop reaches five years of age, but the lower valve community develops more slowly. The adult scallop community shows no variation which can be related to either water depth or season of the year.

9. The activity of borers within the shell is discussed. These play an important role in the development of the community by making

the shell surface habitable for certain later-arriving species.

10. The scallop does not, in general, appear to be harmed by, nor to derive any benefit from, the presence of these organisms upon and within its shell. A possible exception is the case of the boring sponge, *Cliona vastifica*, which may indirectly endanger the life of the scallop by perforating the shell in the hinge region, thus weakening the connection between the valves.

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Addendum:

- Blake, J. A., and J. W. Evans. 1973. *Polydora* and related genera as borers in mollusk shells and other calcareous substrates. *The Veliger* 15(3): 235-249.

APPENDIX 1

TABLE A

EPIBIONTS RECORDED FROM THE SHELLS OF THE TWELVE SCALLOPS
LISTED IN TABLE 2. (PER CENT AREA OCCUPIED = PER
CENT OF TOTAL AREA OCCUPIED BY EPIBIONTS:
NUMBER OF INDIVIDUALS IS GIVEN ONLY WHEN
MEMBERS OF SPECIES ARE COUNTABLE)

TABLE A.1

EPIBIONTS RECORDED FROM SCALLOP NO. 1, UPPER VALVE

Rank by abundance	Species	% Area occupied	No. of Individuals
1	<i>Polydora websteri</i>	41.4	517
2	<i>Lithothamnium glaciale</i>	39.1	-
3	<i>Dodecaceria concharum</i>	14.5	19
4	<i>Polydora concharum</i>	4.75	13
5	<i>Cliona vastifica</i>	0.127	-
6	<i>Anticoma pellucida</i>	0.0844	2
7	Unidentified bivalve	0.0152	9
8	<i>Hiatella arctica</i>	0.0110	3
9	<i>Eggerella advena</i>	0.000338	2
10	<i>Trochammina squamata</i>	0.000253	3

Area of valve = 140.4 cm.²

Total Area occupied by epibionts = 118.5 cm.²

Per cent area occupied by epibionts = 84.4 %.

TABLE A.2

EPIBIONTS RECORDED FROM SCALLOP NO. 1, LOWER VALVE.

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Polydora websteri</i>	41.7	52
2	<i>Cliona vastifica</i>	16.8	-
3	<i>Rhamphostomella ovata</i>	12.0	-
4	<i>Folliculina</i> sp.	9.55	1915
5	<i>Porella aperta</i>	7.78	-
6	<i>Porella</i> sp. B.	7.18	-
7	<i>Cribrilina punctata</i>	1.08	-
8	<i>Membranipora craticula</i>	1.02	-
9	<i>Cylindroporella tubulosa</i>	0.758	-
10	Unidentified scyphozoan	0.548	36
11	<i>Molgula complanata</i>	0.399	2
12	<i>Spirorbis borealis</i>	0.299	2
13	<i>Antithamnion boreale</i>	0.240	-
14	<i>Anticoma pellucida</i>	0.175	6
15	<i>Spirorbis granulatus</i>	0.155	1
16	<i>Noella</i> sp.	0.0998	4
17	<i>Halysarca</i> sp.	0.0798	-
18	<i>Hiatella arctica</i>	0.0599	3
19	<i>Spirorbis spirillum</i>	0.0549	1
20	Unidentified hydroid A.	0.0399	8
21	<i>Trochammina squamata</i>	0.00449	9

Area of valve = 135.4 cm.²Total area occupied by epibionts = 200.4 cm.²

Per cent area occupied by epibionts = 148%.

TABLE A.3

EPIBIONTS RECORDED FROM SCALLOP NO. 2, UPPER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Polydora websteri</i>	65.4	603
2	<i>Lithothamnium glaceale</i>	21.1	-
3	<i>Polydora concharum</i>	6.15	12
4	<i>Dodecaceria concharum</i>	4.28	4
5	<i>Cliona vastifica</i>	0.480	-
6	<i>Hiatella arctica</i>	0.0901	19
7	<i>Anticoma pellucida</i>	0.00593	1

Area of valve = 158.2 cm.²

Total area occupied by epibionts = 84.4 cm.²

Per cent area occupied by epibionts = 53.3%.

TABLE A.4

EPIBIONTS RECORDED FROM SCALLOP NO. 2, LOWER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Schizoporella auriculata</i>	33.8	-
2	<i>Folliculina</i> sp.	17.0	305
3	<i>Haliclona</i> sp.	13.7	-
4	<i>Amphiblestrum osburni</i>	12.8	-
5	* <i>Cribrilina punctata</i>	5.37	-
6	<i>Stomachetosella sinuosa</i>	4.96	-
7	<i>Anomia simplex</i>	3.06	23
8	<i>Rhaphostomella ovata</i>	2.89	-
9	<i>Cylindroporella tubulosa</i>	2.64	-
10	<i>Spirorbis granulatus</i>	1.50	13
11	<i>Spirorbis spirillum</i>	1.44	35
12	<i>Nolella</i> sp.	1.25	34
13	<i>Cliona vastifica</i>	1.11	-
14	<i>Polydora websteri</i>	1.06	3
15	<i>Membranipora craticula</i>	0.891	-
16	<i>Porella</i> sp. A.	0.414	-
17	<i>Tegella armifera</i>	0.388	-
18	<i>Spirorbis violaceus</i>	0.164	4
19	<i>Spirorbis borealis</i>	0.112	1
20	<i>Hiatella arctica</i>	0.104	7
21	<i>Clytia gracilis</i>	0.101	27
22	<i>Anticoma pellucida</i>	0.0559	3
23	<i>Ascidia callosa</i>	0.0559	-
24	<i>Anomia aculeata</i>	0.0559	1
25	<i>Trochammina squamata</i>	0.0224	60
26	Unidentified scyphozoan	0.0209	2
27	Unidentified bivalve	0.00746	1

Area of valve = 148.0 cm.²Total area occupied by epibionts = 26.8 cm.²

Per cent area occupied by epibionts = 18.1%.

TABLE A.5

EPIBIONTS RECORDED FROM SCALLOP NO. 3, UPPER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Polydora websteri</i>	41.2	677
2	<i>Dodecaceria concharum</i>	33.5	58
3	<i>Lithothamnium glaciale</i>	22.3	-
4	<i>Polydora concharum</i>	2.89	10
5	<i>Hiatella arctica</i>	0.0538	21
6	<i>Folliculina</i> sp.	0.00512	8
7	<i>Anticoma pellucida</i>	0.00320	1
8	<i>Lohmanella falcata</i>	0.00256	2
9	Unidentified bivalve	0.00256	2
10	<i>Eggerella advena</i>	0.000512	4
11	<i>Zoothamnion</i> sp.	0.000320	-
12	<i>Trochammina squamata</i>	0.000115	18

Area of valve = 172.4 cm.²

Total Area occupied by epibionts = 156.2 cm.²

Per cent area occupied by epibionts = 90.7%.

TABLE A.6

EPIBIONTS RECORDED FROM SCALLOP NO. 3, LOWER VALVE.

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Haliclona</i> sp.	32.8	-
2	<i>Cribrilina punctata</i>	31.3	-
3	<i>Folliculina</i> sp.	16.3	5075
4	<i>Antithamnion boreale</i>	4.69	-
5	<i>Rhaphostomella ovata</i>	3.19	-
6	<i>Cliona vastifica</i>	2.60	-
7	<i>Halisarca</i> sp.	1.34	-
8	<i>Stomachetosella sinuosa</i>	1.31	-
9	<i>Porella aperta</i>	1.28	-
10	<i>Membranipora craticula</i>	0.849	-
11	<i>Noelella</i> sp.	0.820	51
12	<i>Ascidia callosa</i>	0.772	4
13	Unidentified scyphozoan	0.514	57
14	<i>Cylindroporella tubulosa</i>	0.463	-
15	<i>Molgula complanata</i>	0.386	3
16	<i>Spirorbis spirillum</i>	0.321	4
17	<i>Schizoporella auriculata</i>	0.302	-
18	<i>Anticoma pellucida</i>	0.289	18
19	<i>Spirorbis granulatus</i>	0.199	2
20	<i>Spirorbis violaceus</i>	0.106	3
21	<i>Hiatella arctica</i>	0.103	8
22	<i>Barentsia</i> sp.	0.0608	27
23	<i>Zoothamnion</i> sp.	0.0553	-
24	<i>Trochamnina squamata</i>	0.0344	95
25	<i>Clytia gracilis</i>	0.0289	9
26	<i>Spirorbis vitreus</i>	0.0251	1
27	<i>Balanus</i> sp.	0.0129	1
28	<i>Lichenopora</i> sp.	0.00759	-
29	Unidentified bivalve	0.00643	1
30	<i>Eggerella advena</i>	0.000643	1

Area of valve = 167.4 cm.²Total area occupied by epibionts = 31.1 cm.²

Per cent area occupied by epibionts = 18.6%.

TABLE A.7

EPIBIONTS RECORDED FROM SCALLOP NO. 4, URPER VALVE.

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Polydora websteri</i>	59.9	423
2	<i>Lithothamnium glaciale</i>	25.0	-
3	<i>Dodecaceria concharum</i>	10.8	8
4	<i>Cliona vastifica</i>	2.09	-
5	<i>Polydora concharum</i>	1.94	3
6	<i>Molgula complanata</i>	0.119	2
7	<i>Nolella</i> sp.	0.119	16
8	Unidentified hydroid A	0.0149	10
9	<i>Trochammina squamata</i>	0.00552	37
10	<i>Folliculina</i> sp.	0.00447	3
11	<i>Eggerella advena</i>	0.00179	6
12	<i>Zoothamnion</i> sp.	0.000447	-

Area of valve = 152.0 cm.²Total area occupied by epibionts = 67.1 cm.²

Per cent area occupied by epibionts = 44.2%.

TABLE A.8.

EPIBIONTS RECORDED FROM SCALLOP NO. 4, LOWER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Halictona</i> sp.	26.4	-
2	<i>Folliculina</i> sp.	23.8	5025
3	<i>Tegella armifera</i>	9.40	-
4	<i>Porella aperta</i>	7.88	-
5	<i>Cliona vastifica</i>	6.94	-
6	<i>Cribrilina punctata</i>	1.67	-
7	<i>Membranipora craticula</i>	1.63	-
8	<i>Noella</i> sp.	1.62	679
9	<i>Schizoporella auriculata</i>	0.988	-
10	<i>Porella</i> sp. A	0.969	-
11	<i>Molgula complanata</i>	0.760	4
12	Unidentified schyphozoan	0.598	45
13	<i>Lichenopora</i> sp.	0.584	-
14	<i>Antithamnion boreale</i>	0.451	-
15	<i>Spirorbis granulatus</i>	0.442	3
16	<i>Spirorbis borealis</i>	0.428	3
17	<i>Ascidia callosa</i>	0.285	1
18	<i>Anomia simplex</i>	0.285	4
19	<i>Anticoma pellucida</i>	0.0712	3
20	<i>Trochammina squamata</i>	0.0603	127
21	<i>Spirorbis spirillum</i>	0.0552	1
22	<i>Barentsia</i> sp.	0.0466	14
23	<i>Halisarca</i> sp.	0.0428	-
24	<i>Balanus</i> sp.	0.0190	1

Area of valve = 141.8 cm.²Total area occupied by epibionts = 21.0 cm.²

Per cent area occupied by epibionts = 14.8%.

TABLE A.9

EPIBIONTS RECORDED FROM SCALLOP NO. 5, UPPER VALVE.

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Polydora websteria</i>	59.2	747
2	<i>Lithothamnium glaciale</i>	29.8	-
3	<i>Polydora concharum</i>	8.66	24
4	<i>Dodecaceria concharum</i>	2.26	3
5	<i>Molgula complanata</i>	0.0334	1
6	<i>Eggerella advena</i>	0.0167	94
7	<i>Trochammina squamata</i>	0.0167	20
8	<i>Hiatella arctica</i>	0.0133	4
9	<i>Cliona vastifica</i>	0.00751	-
10	Unidentified ostracod	0.00417	1
11	<i>Anticoma pellucida</i>	0.00417	1
12	<i>Folliculina</i> sp.	0.00167	2

Area of valve = 178.0 cm.²Total area occupied by epibionts = 119.9 cm.²

Per cent area occupied by epibionts = 67.4%.

TABLE A.10

EPIBIONTS RECORDED FROM SCALLOP NO. 5, LOWER VALVE.

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Polydora webateri</i>	32.6	32
2	<i>Cliona vastifica</i>	27.4	-
3	<i>Schizoporella auriculata</i>	12.8	-
4	<i>Noella</i> sp.	5.78	108
5	<i>Porella aperta</i>	4.46	-
6	<i>Folliculina</i> sp.	4.18	390
7	<i>Stomachetosella sinuosa</i>	3.64	-
8	<i>Cribrilina punctata</i>	2.96	-
9	<i>Spirorbis granulatus</i>	2.32	7
10	<i>Porella</i> sp. A	1.71	-
11	<i>Spirorbis borealis</i>	0.964	3
12	<i>Antithamnion boreale</i>	0.428	-
13	<i>Tegella armifera</i>	0.368	-
14	<i>Membranipora craticula</i>	0.107	-
15	<i>Trochamnina squamata</i>	0.106	99
16	Unidentified sphyphozoan	0.0900	3
17	<i>Didemnum albidum</i>	0.0514	-
18	<i>Hiatella arctica</i>	0.0428	1

Area of valve = 174.0 cm.²Total area occupied by epibionts = 9.30 cm.²

Per cent area occupied by epibionts = 5.34%.

TABLE A.11

EPIBIONTS RECORDED FROM SCALLOP NO. 6, UPPER VALVE.

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Polydora websteri</i>	49.2	1126
2	<i>Lithothamnion glaciale</i>	41.7	-
3	<i>Dodecaceria concharum</i>	6.65	16
4	<i>Polydora concharum</i>	1.99	10
5	<i>Acmaea testudinalis</i>	0.207	3
6	<i>Nolella</i> sp.	0.0943	41
7	<i>Cliona vastifica</i>	0.0497	-
8	<i>Porella</i> sp.	0.0253	-
9	<i>Balanus</i> sp.	0.0239	13
10	<i>Antithamnion boreale</i>	0.0230	-
11	<i>Hiatella arctica</i>	0.0221	12
12	<i>Ischnochiton ruber</i>	0.0120	1
13	<i>Eggerella advena</i>	0.00598	38
14	<i>Clytia gracilis</i>	0.00368	8
15	<i>Stauridiosarsia producta</i>	0.00322	7
16	<i>Folliculina</i> sp.	0.00322	7
17	Unidentified bivalve	0.00276	3
18	<i>Anticoma pellucida</i>	0.00230	1
19	<i>Trochammina squamata</i>	0.00124	27

Area of valve = 168.4 cm.²Total area occupied by epibionts = 217.4 cm.²

Per cent area occupied by epibionts = 129%.

TABLE A.12

EPIBIONTS RECORDED FROM SCALLOP NO. 6, LOWER VALVE.

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Haliclona</i> sp.	26.3	7
2	<i>Folliculina</i> sp.	23.6	4631
3	<i>Glyona vastifica</i>	16.8	-
4	<i>Porella aperta</i>	14.8	-
5	<i>Rhaphostomella ovata</i>	4.63	-
6	<i>Spirorbis granulatus</i>	2.69	17
7	<i>Antithamnion boreale</i>	2.36	-
8	<i>Polydora concharum</i>	2.21	1
9	<i>Nolella</i> sp.	1.86	73
10	<i>Stomachetosella sinuosa</i>	1.77	-
11	<i>Membranipora craticula</i>	0.571	-
12	<i>Porella</i> sp. A	0.399	-
13	<i>Didemnum albidum</i>	0.362	-
14	<i>Barentsia</i> sp.	0.282	79
15	<i>Spirorbis spirillum</i>	0.281	5
16	<i>Amphiblestrum osburni</i>	0.228	-
17	<i>Molgula complanata</i>	0.204	1
18	<i>Cylindroporella tubulosa</i>	0.165	-
19	<i>Stauridiosarsia producta</i>	0.0918	-
20	<i>Anomia simplex</i>	0.0765	1
21	<i>Spirorbis violaceus</i>	0.0561	1
22	Unidentified hydroid B	0.0561	11
23	<i>Anticoma pellucida</i>	0.0510	2
24	<i>Cribrellina punctata</i>	0.0408	-
25	<i>Hiatella arctica</i>	0.0408	2
26	<i>Trochammia squamata</i>	0.0301	59
27	<i>Amphiascus</i> sp.	0.0255	1
28	<i>Lohmannella falcata</i>	0.0102	1
29	Unidentified bivalve	0.0102	1
30	<i>Eggerella advena</i>	0.00204	2

Area of valve = 164.4 cm.²Total area occupied by epibionts = 19.6 cm.²

Per cent area occupied by epibionts = 12.0%.

TABLE A.13

EPIBIONTS RECORDED FROM SCALLOP NO. 7, UPPER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Lithothamnium glaciale</i>	44.7	-
2	<i>Polydora websteri</i>	43.6	578
3	<i>Dodecaceria concharum</i>	8.60	12
4	<i>Polydora concharum</i>	2.40	7
5	<i>Anomia simplex</i>	0.232	3
6	<i>Balanus</i> sp.	0.146	46
7	<i>Cliona vastifica</i>	0.114	-
8	<i>Antithamnion boreale</i>	0.0415	-
9	<i>Nolella</i> sp.	0.0278	7
10	<i>Stauridiosarsia producta</i>	0.0246	31
11	<i>Spirorbis granulatus</i>	0.0246	1
12	<i>Lichenopora</i> sp.	0.0216	-
13	<i>Hiattella arctica</i>	0.00953	3
14	<i>Spirorbis spirillum</i>	0.00873	1
15	<i>Trochammina squamata</i>	0.00476	6
16	Unidentified bivalve	0.00318	2
17	Unidentified hydroid A	0.00159	2
18	<i>Eggerella advena</i>	0.000873	11

Area of valve = 134.4 cm.²

Total area occupied by epibionts = 125.9 cm.²

Per cent area occupied by epibionts = 94.0%.

TABLE A.14

EPIBIONTS RECORDED FROM SCALLOP NO. 7, LOWER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Haliclona</i> sp.	9.79	-
2	<i>Schizoporella auriculata</i>	9.05	-
3	<i>Cliona vastifica</i>	3.96	-
4	<i>Folliculina</i> sp.	3.06	4077
5	<i>Molgula citrina</i>	2.62	4
6	<i>Lithothamnium glaciale</i>	2.43	-
7	<i>Membranipora craticula</i>	2.39	-
8	<i>Tegella arctica</i>	1.47	-
9	<i>Rhynchostomella ovata</i>	1.31	-
10	<i>Tegella armifera</i>	1.17	-
11	<i>Spirorbis granulatus</i>	1.10	47
12	<i>Cribrilina punctata</i>	0.580	-
13	<i>Stomachetosella sinuosa</i>	0.566	-
14	<i>Nolella</i> sp.	0.413	110
15	<i>Polydora websteri</i>	0.357	5
16	<i>Didemnum albidum</i>	0.320	-
17	<i>Porella aperta</i>	0.255	-
18	<i>Halisarca</i> sp.	0.204	-
19	<i>Cylindroporella tubulosa</i>	0.159	-
20	Unidentified hydroid A	0.143	191

TABLE A.14 (CONTINUED)

Rank by abundance	Species	% Area occupied	No. of individuals
21	<i>Antithamnion boreale</i>	0.143	-
22	<i>Lichenopora</i> sp.	0.0991	-
23	<i>Balanus</i> sp.	0.0540	18
24	<i>Spirorbis borealis</i>	0.0450	2
25	<i>Porella</i> sp. A	0.0388	-
26	<i>Trochammina squamata</i>	0.0255	34
27	<i>Anomia simplex</i>	0.0225	2
28	<i>Ischnochiton ruber</i>	0.0195	2
29	<i>Spirorbis violaceus</i>	0.0165	2
30	<i>Anticoma pellucida</i>	0.0113	3
31	<i>Hiatella arctica</i>	0.00901	3
32	<i>Spirorbis spirillum</i>	0.00826	1
33	<i>Barentsia</i> sp.	0.00315	6
34	<i>Stauridiosarsia producta</i>	0.00300	4
35	Unidentified bivalve	0.00150	1
36	<i>Sarsia tubulosa</i>	0.00150	2
37	<i>Eggerella advena</i>	0.000450	3

Area of valve = 133.2 cm.²

Total area occupied by epibionts = 55.8 cm.²

Per cent area occupied by epibionts = 42.0%

TABLE A.15

EPIBIONTS RECORDED FROM SCALLOP NO. 8, UPPER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Lithothamnium glaciale</i>	44.0	-
2	<i>Polydora websteri</i>	33.4	16
3	<i>Dodecaceria concharum</i>	19.8	1
4	<i>Cliona vastifica</i>	2.77	-
5	<i>Clytia gracilis</i>	0.0220	1
6	<i>Eggerella advena</i>	0.00440	1
7	<i>Trochammina squamata</i>	0.00220	2

Area of valve = 98.0 cm.²

Total area occupied by epibionts = 45.5 cm.²

Per cent area occupied by epibionts = 46.5%.

TABLE A.16

EPIBIONTS RECORDED FROM SCALLOP NO. 8, LOWER VALVE.

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Halisarca</i> sp.	80.2	-
2	<i>Folliculina</i> sp.	12.5	5955
3	<i>Membranipora craticula</i>	4.13	-
4	<i>Cliona vastifica</i>	1.76	-
5	<i>Tegella armifera</i>	0.700	-
6	<i>Polydora websteri</i>	0.598	3
7	<i>Clytia gracilis</i>	0.0797	38
8	<i>Anomia simplex</i>	0.0314	1
9	<i>Cribrilina punctata</i>	0.0147	-
10	<i>Trochammina squamata</i>	0.000629	3

Area of valve = 91.2 cm.²Total area occupied by epibionts = 47.7 cm.²

Per cent area occupied by epibionts = 52.3%.

TABLE A.17

EPIBIONTS RECORDED FROM SCALLOP NO. 9, UPPER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Lithothamnium glaciale</i>	93.8	-
2	<i>Polydora websteri</i>	5.37	2
3	<i>Clytia gracilis</i>	0.480	17
4	<i>Folliculina</i> sp.	0.169	6
5	<i>Membranipora craticula</i>	0.155	-
6	<i>Trochammina squamata</i>	0.00282	1

Area of valve = 56.8 cm.²

Total area occupied by epibionts = 3.54 cm.²

Per cent area occupied by epibionts = 6.24%.

TABLE A.18

EPIBIONTS RECORDED FROM SCALLOP NO. 9, LOWER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Folliculina</i> sp.	79.4	4288
2	<i>Membranipora craticula</i>	16.8	-
3	<i>Barentsia</i> sp.	1.24	96
4	<i>Cliona vastifica</i>	0.500	-
5	<i>Cribrilina punctata</i>	0.500	-
6	<i>Lichenopora</i> sp.	0.444	-
7	<i>Cylindroporella tubulosa</i>	0.444	-
8	<i>Porella</i> sp. A	0.278	-
9	<i>Hiatella arctica</i>	0.222	3
10	<i>Spirorbis spirillum</i>	0.204	1
11	Unidentified bivalve	0.0370	1
12	<i>Clytia gracilis</i>	0.0370	2
13	<i>Zoothamnion</i> sp.	0.00556	3
14	<i>Trochammina squamata</i>	0.00185	17

Area of valve = 50.4 cm.²

Total area occupied by epibionts = 5.4 cm.²

Per cent area occupied by epibionts = 10.7%.

TABLE A.19

EPIBIONTS RECORDED FROM SCALLOP NO. 10, UPPER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Antithamnion boreale</i>	61.1	-
2	<i>Lithothamnion glaciale</i>	30.5	-
3	<i>Folliculina</i> sp.	8.40	11
4	<i>Trochammina squamata</i>	0.0763	1

Area of valve = 30.8 cm.²Total area occupied by epibionts = 1.3 cm.²

Per cent area occupied by epibionts = 4.22%

TABLE A.20

EPIBIONTS RECORDED FROM SCALLOP NO. 10, LOWER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Folliculina</i> sp.	52.5	463
2	<i>Lithothamnium glaciale</i>	31.1	-
3	<i>Antithamnion boreale</i>	7.26	-
4	<i>Anticoma pellucida</i>	3.97	7
5	<i>Barentsia</i> sp.	3.65	46
6	<i>Membranipora craticula</i>	1.02	-
7	<i>Hiatella arctica</i>	0.454	1
8	<i>Trochammina squamata</i>	0.0454	4

Area of valve = 29.4 cm.²Total area occupied by epibionts = 8.80 cm.²

Per cent area occupied by epibionts = 29.8%

TABLE A.21

EPIBIONTS RECORDED FROM SCALLOP NO. 11, UPPER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Lithothamnium glaciale</i>	58.4	2
2	<i>Polydora websteri</i>	37.8	540
3	<i>Dodecaceria concharum</i>	1.33	2
4	<i>Polydora concharum</i>	1.27	4
5	<i>Cliona vastifica</i>	0.920	-
6	<i>Folliculina</i> sp.	0.0655	89
7	<i>Spirorbis grammatus</i>	0.0456	2
8	<i>Spirorbis borealis</i>	0.0442	4
9	<i>Anomia simplex</i>	0.0331	3
10	<i>Ischnochiton ruber</i>	0.0317	2
11	<i>Molgula complanata</i>	0.0294	1
12	<i>Antithamnion boreale</i>	0.0221	-
13	<i>Membranipora craticula</i>	0.00861	-
14	<i>Spirorbis spirillum</i>	0.00810	1
15	<i>Trochamnina squamata</i>	0.00604	82
16	<i>Hiatella arctica</i>	0.00589	2
17	<i>Anticoma pellucida</i>	0.00368	1
18	<i>Lichenopora</i> sp.	0.00353	-
19	<i>Haliclona</i> sp.	0.00353	-
20	<i>Balanus</i> sp.	0.00294	1
21	<i>Eggerella advena</i>	0.00162	11
22	<i>Clytia gracilis</i>	0.000736	1

Area of valve = 164.6 cm.²Total area occupied by epibionts = 135.9 cm.²

Per cent area occupied by epibionts = 82.4%

TABLE A.22

EPIBIONTS RECORDED FROM SCALLOP NO. 11, LOWER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Haliclona</i> sp.	28.3	-
2	<i>Schizoporella auriculata</i>	25.7	-
3	<i>Folliculina</i> sp.	13.3	4184
4	<i>Cliona vastifica</i>	9.58	-
5	<i>Stomachetosella sinuosa</i>	4.93	-
6	<i>Membranipora craticula</i>	3.37	-
7	<i>Rhynchostomella ovata</i>	3.31	-
8	<i>Lithothamnium glaciale</i>	2.32	-
9	<i>Spirorbis granulatus</i>	2.07	21
10	<i>Porella</i> sp. A.	2.06	-
11	<i>Halisarca</i> sp.	1.37	-
12	<i>Didemnum albidum</i>	0.968	-
13	<i>Tegella armifera</i>	0.952	-
14	<i>Antithamnion boreale</i>	0.630	-
15	<i>Cribrilina punctata</i>	0.624	-
16	<i>Anomia simplex</i>	0.239	5
17	<i>Spirorbis spirillum</i>	0.0700	2
18	<i>Hiatella arctica</i>	0.0637	5
19	<i>Spirorbis violaceus</i>	0.0350	1
20	<i>Lichenopora</i> sp.	0.0258	-
21	<i>Trochammina squamata</i>	0.0181	57
22	Unidentified hydroid A	0.0159	5
23	<i>Amphiascus</i> sp.	0.0159	1
24	<i>Balanus</i> sp.	0.0127	1
25	<i>Eggerella advena</i>	0.00191	3

Area of valve = 158.6 cm.²Total area occupied by epibionts = 31.4 cm.²

Per cent area occupied by epibionts = 19.8%.

TABLE A.23

EPIBIONTS RECORDED FROM SCALLOP NO. 12, UPPER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Polydora websteri</i>	42.6	190
2	<i>Lithothamnium glaciale</i>	36.8	-
3	<i>Dodecaceria concharum</i>	10.6	5
4	<i>Polydora concharum</i>	9.28	28
5	<i>Antithamnion boreale</i>	0.274	-
6	<i>Folliculina</i> sp.	0.116	49
7	<i>Spirorbis borealis</i>	0.0708	1
8	<i>Anomia simplex</i>	0.0354	1
9	<i>Membranipora craticula</i>	0.0307	-
10	<i>Cliona vastifica</i>	0.0298	2
11	<i>Lichenopora</i> sp.	0.0264	-
12	<i>Eggerella advena</i>	0.0132	28
13	<i>Hiatella arctica</i>	0.00945	1
14	<i>Trochammina squamata</i>	0.00402	17

Area of valve = 135.2 cm.²

Total area occupied by epibionts = 42.3 cm.²

Per cent area occupied by epibionts = 31.3%.

TABLE A.24

EPIBIONTS RECORDED FROM SCALLOP NO. 12, LOWER VALVE

Rank by abundance	Species	% Area occupied	No. of individuals
1	<i>Folliculina</i> sp.	24.0	5599
2	<i>Porella</i> sp. A	14.6	-
3	<i>Haliclona</i> sp.	14.5	-
4	<i>Halisarca</i> sp.	6.18	-
5	<i>Membranipora craticula</i>	5.41	-
6	<i>Spirorbis granulatus</i>	5.32	40
7	<i>Tegella armifera</i>	4.10	-
8	<i>Lichenopora</i> sp.	3.14	-
9	<i>Cliona vastifica</i>	3.02	-
10	<i>Antithamnion boreale</i>	2.98	-
11	<i>Nolella</i> sp.	2.34	109
12	<i>Polydora websteria</i>	2.04	5
13	<i>Cribrilina punctata</i>	1.79	-
14	<i>Molgula complanata</i>	1.70	4
15	<i>Stomachetosella sinuosa</i>	1.24	-
16	<i>Didemnum albidum</i>	1.18	-
17	<i>Porella aperta</i>	0.794	-
18	<i>Schizoporella auriculata</i>	0.369	-
19	<i>Cylindroporella tubulosa</i>	0.350	-
20	<i>Spirorbis borealis</i>	0.258	2

TABLE A.24 (CONTINUED)

Rank by abundance	Species	% Area occupied	No. of individuals
21	<i>Ascidia callosa</i>	0.258	1
22	<i>Anomia simplex</i>	0.193	3
23	<i>Spirorbis spirillum</i>	0.142	3
24	Unidentified schyphozoan	0.120	10
25	Unidentified hydroid A	0.0945	22
26	<i>Trochammina squamata</i>	0.0661	172
27	<i>Anticoma pellucida</i>	0.0429	2
28	<i>Amphiascus</i> sp.	0.0215	1
29	<i>Balanus</i> sp.	0.0172	1
30	<i>Barentsia</i> sp.	0.0150	5
31	<i>Clytia gracilis</i>	0.0129	3
32	<i>Eggerella advena</i>	0.00773	12

Area of valve = 127.4 cm.²

Total area occupied by epibionts = 23.3 cm.²

Per cent area occupied by epibionts = 18.3%.

APPENDIX 2

APPENDIX 2

Other Symbionts of *P. magellanicus*

In the course of examining some of the live scallops which had been maintained in the laboratory, two other organisms were detected. These were not normally found associated with the shell, but rather with the scallop itself. For this reason they have been excluded from the list of epibionts on the shell and are mentioned only briefly here.

The first of these was a tiny white or cream-coloured rhabdocoel (Platyhelminthes: Turbellaria). This animal was usually found on the gills of live scallops, where it moved quickly amongst the gill filaments. Occasionally it was noticed in the vicinity of the edge of the mantle, and in one instance it was seen swimming around the edge of the shell. However, this flatworm is not believed to be normally associated with the shell. Scott (1968) also mentioned this organism, stating that it was found on the gills of scallops from Salmonier Arm and from one other location. It has been tentatively identified as *Paravortex gemellipara* (Linton, 1910).

The other animal was ciliated protozoan, believed to be a member of the Order Peritricha. It was colourless, vase-shaped and about 150 μ in length. The anterior disc was approximately 70 to 80 μ in diameter and the stem was contractile with an enlarged basal extension. The latter appeared to have a concave lower surface, contact with the substrate being maintained by its two ciliated edges. This organism was found in large numbers on the mantle edge, tentacles and eyes of

some of the live scallops maintained in the laboratory. It has not been identified.

A unicellular alga, as yet unidentified, has been reported from *P. magellanicus* in the Newfoundland area. It was first noted by Naidu (1969), mainly in certain tissues of the mantle. Stevenson (1972) placed the alga in the Class Chlorophyceae, Order Chlorococcales, and believed that it probably belonged in either the Family Coccomyxaceae or the Family Oocystaceae. Besides the more obvious infection in the mantle, Stevenson also found the alga in the gill filaments, the adductor muscle and the anal region; within certain blood cells; and within phagocytes in infected tissues. Infection is believed by him to occur via the digestive system.

REFERENCES CITED IN APPENDIX 2

- Naidu, K. S. 1969. Growth, reproduction, and unicellular symbiotic alga in the giant scallop, *Placopecten magellanicus* (Gmelin), in Port au Port Bay, Newfoundland. M.Sc. Thesis. Memorial University of Newfoundland. 181 pp.
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